

**EFFECTS OF TOXICANTS ON BIOLOGICAL SPECIES :
SOME NON – LINEAR MATHEMATICAL MODELS
AND THEIR ANALYSIS**

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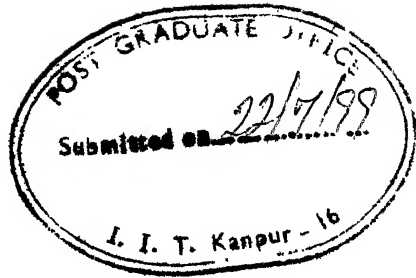
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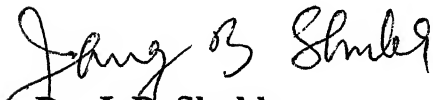


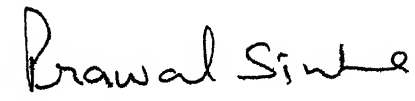
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Certificate



It is certified that the work contained in the thesis entitled "*Effects of toxicants on biological species : Some non - linear mathematical models And their analyses*", by Mr. Alok Kumar Agrawal, has been carried out under our supervision and that this work has not been submitted to any other Institution for a degree.


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Dedicated to

Rai Saheb

and my Parents

Smt. Radha Rani Agrawal

and

Late Shree R. D. Agrawal

With

Profound Respect

Synopsis

It is well known in ecotoxicological studies that biological species in both the terrestrial and aquatic ecosystems are affected when their habitats are stressed by toxicants emitted into the environment. In general, these toxicants (pollutants) are emitted from industrial and household sources, exhausts from vehicles or these may be produced by species itself. The effect of toxicant is to decrease the growth and productivity of the affected species as well as the carrying capacity of the environment.

In past several decades, mathematical models have become important tool to analyze and predict the behavior of ecological systems but modelling the effects of toxicants on biological populations in both aquatic and terrestrial environments is a relatively new area of research in ecotoxicology. It may be pointed out further that most of the studies in past have been experimental and efforts to understand these phenomena using mathematical models have been limited. Therefore, the aim of this thesis is to propose new mathematical models which break new grounds or illustrate the importance of some new aspects of significant interest and relevant to both new and old phenomena.

Specifically, the models for the following situations are described:

- Effect of a single toxicant on a biological species.
- Simultaneous effect of two or more toxicants on a biological species
- Simultaneous effect of two toxicants on a biological species when a secondary toxicant is formed.
- Effect of a toxicant produced by a plant species on the other competing species : The case of Allelopathy.
- Effect of a toxicant on two competing biological species.
- Effect of a toxicant on a biological population, a subclass of which exhibits severe symptoms such as reduction in size, deformity, lesion, etc.

The models proposed here consist of system of non-linear ordinary differential equations. For each model, the existence and uniqueness of positive equilibria are discussed. Further, the local stability behavior of these equilibria is discussed using variational matrix method and Hurwitz criterion. In some cases, where it becomes difficult to apply Hurwitz criterion, the linearization technique and method of Lyapunov's functions have been used to find sufficient conditions for the local asymptotic stability of positive equilibria. The global stability behavior of positive equilibria has been studied by using Lyapunov's method and sufficient conditions for global asymptotic stability of positive equilibria are found.

The thesis consists of nine Chapters, in all. The first Chapter consists of general introduction and literature survey.

In Chapter II, a mathematical model for the effect of a single toxicant on a biological species, when the toxicant is being emitted by the biological species itself, has been proposed and analyzed. A general case in which, this toxicant is produced by the biological species as well as emitted in to the environment by some external source has also been considered. It has been shown that if the emission rate of the toxicant increases, the equilibrium level of the biological population decreases. It has been noted that for large emission rate, the population may be driven to extinction. Further, it is noted that under certain conditions, there may exist oscillation in the system for an appropriate choice of the growth rate and carrying capacity functions of the biological species.

In Chapter III, a mathematical model to study the simultaneous effect of two toxicants on a biological population, when one toxicant is produced in the environment by the biological species and the other is emitted in to the environment by some external source has been proposed and analyzed under the assumption that the toxicities of the two toxicants may be different. It has been found that in the case of constant emission of the toxicant from an external source, the population settles down to an equilibrium level, which is lower than its initial (toxicant independent) carrying capacity and is also lower than that in the case of instantaneous emission, the magnitude of which depends upon the toxicity, emission and washout rates of each of the

toxics and on the emission rate coefficient by which the second toxicant is being discharged in the environment by the biological population. It is noted that this equilibrium decreases as the toxicity and the emission rates of the two toxicants from the external source as well as by the species, increase and is always lower than the case of single toxicant having the same characteristics as one of them.

There may exist situations, in which, a part of the toxicant is converted in to another toxicant and both the toxicants (primary and secondary) are harmful to the biological species in the habitat e.g. Sulphur dioxide and sulphuric acid. In Chapter IV, we have proposed and analyzed the simultaneous effect of primary and secondary toxicants on a biological population. It is considered that the primary toxicant is being emitted in to the environment by some external source. The results found in this Chapter, are similar to the results of Chapter III. It has also been pointed out in this Chapter, that the biological species is doomed to extinction if the emission rate of the primary toxicant is very large and the secondary toxicant is equally harmful.

In Chapter V, we have presented a mathematical model for studying the simultaneous effects of a number of toxicants emitted into the environment from different sources, on a biological population. The conclusions drawn in this Chapter, are also similar to those in Chapters - III and IV. It has been found that in the case of uncontrolled continuous emissions of toxicants with large influx rates, the affected biological population may be doomed to extinction sooner than the case of a single toxicant or simultaneous effect of two toxicants, other parameters in the system being the same. It is also pointed out here that as the number of toxicants and their toxicity increase, the density of the affected population decreases further.

In Chapter VI, a nonlinear mathematical model to study the allelopathic effects between two competing biological species has been proposed and analyzed. It has been shown that the equilibrium level of the affected species decreases as the rate of production of the toxicant by the other species increases. It is also noted that if the toxicants are produced continuously in the environment without control, the affected species is doomed to extinction.

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In Chapter V, we have presented a mathematical model for studying the simultaneous effects of a number of toxicants emitted into the environment from different sources, on a biological population. The conclusions drawn in this Chapter, are also similar to those in Chapters - III and IV. It has been found that in the case of uncontrolled continuous emissions of toxicants with large influx rates, the affected biological population may be doomed to extinction sooner than the case of a single toxicant or simultaneous effect of two toxicants, other parameters in the system being the same. It is also pointed out here that as the number of toxicants and their toxicity increase, the density of the affected population decreases further.

In Chapter VI, a nonlinear mathematical model to study the allelopathic effects between two competing biological species has been proposed and analyzed. It has been shown that the equilibrium level of the affected species decreases as the rate of production of the toxicant by the other species increases. It is also noted that if the toxicants are produced continuously in the environment without control, the affected species is doomed to extinction.

In Chapter VII, a mathematical model is proposed and analyzed to study the effect of a toxicant emitted in to the environment from an external source on two competing biological species. It is shown that in the case of instantaneous influx of toxicant, the densities of the competitive species will decrease initially but may recover back to their equilibrium states provided the washout rate of the toxicant is small, however this may take a long time. In the case of constant influx of toxicant, it is shown that the competitive species will settle down to their respective equilibrium levels under certain conditions and their magnitudes will be lower than their initial carrying capacities and these will depend upon its influx and washout rates. The analysis also suggests that the usual competition outcomes may be altered between the two competing biological species.

In Chapter VIII, a mathematical model is proposed and analyzed to study the effect of a toxicant on two competing species as in Chapter VII, when the toxicant is being produced by one of the species itself. It is shown that the competitive species will settle down to their respective equilibrium levels under certain conditions and their magnitudes will be lower than their initial carrying capacities and these will depend upon the influx and washout rates of the toxicant discharged by the species in to the environment. It is also pointed out that the survival of both the competing species will be threatened if the toxicant continues to be produced unabatedly by the species.

In Chapter IX, a mathematical model is proposed and analyzed to study the effect of a toxicant on a biological species, a subclass of which shows abnormal symptoms such as deformity, necrosis, etc. It has been shown that under instantaneous emission of the toxicant, the system gets restored to its original state but after a long time. However under constant emission, under certain conditions, the species would settle down to its equilibrium value whose magnitude is less than its original carrying capacity. It is also found that a subclass of this species, which is severely affected and shows abnormal symptoms, also settles down to its equilibrium level but the magnitude of this equilibrium level increases as the emission rate of the toxicant increases. For large emission rate it may happen that the entire population gets severely affected and become abnormal (different from the original species).

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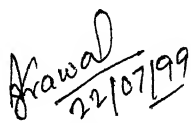
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CHAPTER I

GENERAL INTRODUCTION

1. INTRODUCTION

It is well known in ecotoxicological studies that biological populations in both the terrestrial and aquatic ecosystems are affected when their habitats are stressed by toxicants emitted into the environment (Nelson, 1970; Kozlowski, 1975; Constantinidou and Kozlowski, 1979,a,b; Kozlowski, 1980; Hass, 1981; Jenson and Marshall, 1982; Patin, 1982). In general, these toxicants (pollutants) are emitted from industrial and household sources, exhausts from vehicles or these may be produced by species itself (Jorgensen, 1957; Grab, 1961; Rescigno, 1977; Rice, 1984; jaykumar et al, 1987a,b; Eyini et al, 1989; Chung and Miller, 1995). The effect of toxicant, in general, is to reduce the growth and productivity of the affected species as well as its carrying capacity with respect to the environment.

There are many examples of how toxicants (air pollutants) can destroy/change the character and productivity of vast areas of forest, agricultural crops and vegetations (Todd and Garber, 1958; Treshow, 1968; Davis, 1972; Kozlowski, 1975; Manning, 1975; Pack and Sulzback, 1976; Constantinidou and Kozlowski, 1979,a,b; Kozlowski, 1980; Garsed et al, 1981; Henriksson and Pearson, 1981; Norby and Kozlowski, 1981; Reinert and Gray, 1981; Smith, 1981; Hosker and Lindberg, 1982; Stan and Schicker, 1982; McLaughlin, 1985; Singh et al, 1985; Yunus et al, 1985; Singh et al, 1988; Singh et al, 1990; Singh and Rai, 1991; Shukla and Dubey, 1996;

Shukla et al, 1996; Tichy, 1996). Hosker and Lindberg (1982) presented a review of deposition of gases and particles from the atmosphere induced by plant assimilation. Gaseous pollutants (toxicants) absorbed through plant stomata, injure its leaves and acute injury is followed after rapid absorption of more toxicants which kills tissues. During or soon after exposure leaf cells collapse, necrotic patterns subsequently appear. Chronic injury is caused by rapid absorption, over a long period of sublethal amounts of toxicants and is characterized by chlorosis, which develops slowly and is associated with early leaf senescence. Sometimes, (Kozlowski, 1975,1980) chronic injury is accompanied by necrotic markings (lesions). There is considerable evidence that growth of trees is also reduced by air pollutants because of lowered availability of metabolites at growth sites. The gases such as SO₂ and O₃ affect plant metabolism rapidly (Treshow, 1968; Kozlowski, 1975; Constantinidou and Kozlowski, 1979,a,b; Kozlowski, 1980; Reinert and Gray, 1981; Smith, 1981; Singh et al, 1990).

In the following, we give a brief literature survey of the research already done and relevant to the thesis work.

2. EFFECTS OF TOXICANTS (POLLUTANTS) ON BIOLOGICAL SPECIES IN TERRESTRIAL ECOSYSTEMS: EXPERIMENTAL STUDIES

The effects of air pollutants (toxicants) on plant species have been studied extensively, mainly experimentally (Todd and Garber, 1958; Treshow, 1968; Davis, 1972; Kozlowski, 1975; Manning, 1975; Saunders, 1975; Pack and Sulzback, 1976; Shriner, 1977; Kozlowski, 1980; Garsed et al, 1981; Norby and Kozlowski, 1981; Maclean and Schneider, 1981; Reinert and Gray, 1981; Smith, 1981;

Stan and Schicker, 1982; McLaughlin, 1985; Singh et al, 1985; Yunus et al, 1985; Kozlowski, 1986; Singh et al, 1988; Rai and Raizada, 1989; Singh et al, 1990; Singh and Rai, 1991; Tichy, 1996). In particular, the effects of air pollutants on the growth and productivity of plant populations have been investigated by Todd and Garber (1958), Treshow (1968). The effects of sulphur dioxide on plant yield, growth, photosynthesis and respiration have been studied by Davis (1972), Garsed et al. (1981). Norby and Kozlowski (1981) studied the relative sensitivity of three species of woody plants to sulphur dioxide. Rai and Raizada (1989) studied the effect of bimetallic combinations of Cr, Ni and Pb on the growth of *nostic muscorum*. The effects of ozone and hydrogen fluoride on yield, leaf necrosis, etc. have been investigated by Maclean and Schneider (1981), Stan and Schicker (1982). The effect of plant fruiting to hydrogen fluoride fumigation has been investigated by Pack and Sulzback (1976) and the response of radish to nitrogen dioxide, sulphur dioxide and ozone alone and in combination has been investigated by Reinert and Gray (1981). Manning (1975) has studied interactions between air pollutants and fungal, bacteria and viral plant pathogens. The effect of simulated rain-acidified with sulfuric acid on host parasite interactions has been investigated by Shriner (1977).

It is noted that in most experimental studies, the source of toxicant emission into the environment is external. However, there are situations in the plant kingdom, as in the case of allelopathy, where toxicants may be produced by a plant species affecting the other competing plant species in the habitat, (Rice, 1984). Abdul

Rahman and Habib (1989) studied the allelopathic effect of alfalfa *Medicago sativa* on bladygrass (*Imperata cylindrica*). It has been noted that in such a case, plant roots and leaves play an important role in producing toxicants (Jaykumar et al, 1987a,b; Eyini et al, 1989). Although, the quantity of the toxicant, produced by the plant, is not very large, it is enough to exert strong influence on the soil micro flora and to affect significantly the growth of the source as well as neighboring plants.

3. EFFECTS OF TOXICANTS ON BIOLOGICAL SPECIES IN AQUATIC ECOSYSTEMS: EXPERIMENTAL STUDIES

In the above, we have briefly reviewed some relevant experimental work related to effects of toxicants on terrestrial ecosystems, mainly plant population. However, there have been several investigations related to the effect of a single toxicant or two toxicants in combination including interactive effects on biological species in aquatic environment (Nelson, 1970; Oliver, 1973; Wallis, 1975; Armstrong and Scott, 1979; Driscoll et al, 1980; Moulder, 1980; Sanders and Windom, 1980; Stromgren, 1980; Fisher and Jones, 1981; Karickhoff, 1981; Klumpy and Peterson, 1981; Konemann, 1981; MacInnes, 1981; Muhlbaier and Tissue, 1981; Parker, 1981; Rainer and Fitzhardinge, 1981; Rao, 1981; Thompson and Ho, 1981; Patin, 1982; Brown, 1983; Stratton, 1983; Aoyama and Okamura, 1984; Kvoigman and Metz, 1984; Hunn, 1985; Cairns, 1985; Metz and Dickmann, 1986; Aoyama et al, 1987; Barber et al, 1988; Cairns et al, 1990; Dickman et al, 1990a,b; Atlas et al, 1991; Munkittrick et al, 1991; Dickman et al, 1992; Woin and Bronmark, 1992; Aoyama and Okamura, 1993; Hartwell et al, 1993; Okamura and

Aoyama, 1994; Lin and Chen, 1996; Aidar et al, 1997; Fernandes, 1997; Francesconi et al, 1997; Hall et al, 1997; Hyne and Wilson, 1997; Walsh and O'halloran, 1997; Widdows et al, 1997; Kiceniuk et al, 1997; Perez-Coll et al, 1997; Blockwell et al, 1998; Henry et al, 1998). In particular, Armstrong and Scott (1979) have studied the mercury contents of fishes in Ball Lake, Ontario and found that level of mercury has decreased since imposition of controls on mercury discharge. Patin (1982) has described the effects of various toxicants (pollutants) such as petroleum products, heavy metals on marine algae. Lin and Chen (1996) studied the effects of heavy metal (Zn, Cu or Cd) pollution on oyster samples collected from a coastal area in Taiwan near a major electro - plating industry and showed that the concentrations of these metals were two to five times higher in oyster in the study region in comparison to other regions in Taiwan. Widdows et al (1997) studied sampled mussels in various parts of the Venice Lagoon stressed by chemical toxicants (Cr, Hg, Ni, Cd, Fe, Mn or chlorinated hydrocarbons, etc.) and found a significant reduction in their growth as compared to those living in other regions of the Lagoon.

In some situations in aquatic systems, a toxicant produced by an aquatic species (say algae) not only affects the other species in the aquatic habitat but affects itself also, (Jorgensen, 1957; Abdul Rahman and Habib, 1989). In particular, Jorgensen (1957) found that the algae form some substances which inhibit the growth of these algae as well as of other aquatic species.

In the above studies, it has been postulated that the members of the species affected by toxicants show similar symptoms.

However, there are some situations where a subclass of the total population caused by acute toxicity exhibits severe symptoms in the form of size, deformity, etc. in aquatic populations (Hamilton and Saether, 1971; Woin and Bronmark, 1992; Cushman, 1984; Warwick, 1985; Hartwell *et al*, 1993; Dickman and Rygiel, 1996). For example, Woin and Bronmark (1992) studied the effect of DDT and MCPA on reproduction of snail collected from eutrophic pond in southern Sweden and showed that these pollutants may have no effect on mortality but have profound effect on the distribution and abundance of the species through a reduction in the reproductive potential. Hartwell *et al* (1993) studied the growth of *Eurytemora affinis* (Copepoda) in flow through chambers at different locations of polluted sites in Chesapeake Bay tributaries and found that growth rate and fecundity may be chosen as indicators of water quality at appropriate locations and in between the locations. Dickman and Rygiel (1996) studied the effects of heavy metals and oily wastes discharged from a stainless steel company in the Niagara River on an invertebrate population of midge (chironomid) larvae and found that 26 % of the chironomids from sites located 10 to 800 m down stream were deformed.

4. EFFECTS OF TWO OR MORE TOXICANTS ON BIOLOGICAL SPECIES: EXPERIMENTAL STUDIES

It is noted that majority of the studies reported in literature deal with the biological effect of single toxicant whereas under actual conditions the species is invariably acted upon by several toxicants simultaneously (Patin, 1982; Cairns,

1985; Cairns *et al*, 1990; Atlas *et al*, 1991; Hyne and Wilson, 1997). Patin (1982) has described the combined effect of two pollutants such as petroleum product with DDT, metals and detergents, etc. on phytoplankton and other aquatic organisms. Synergistic effects have been observed for the combinations of petroleum with DDT and certain metal with detergent. It has been noted that a combined effect of several metals may be additive or else it may be manifested by a dominant inhibitory effect. Cairns *et al* (1990) evaluated the joint toxicity effect of chlorine and ammonia on aquatic communities alone and in combinations. They have shown that the species richness of protozoans decreased about 20 % with increasing toxicant concentrations. Atlas *et al* (1991) studied the response of microbial populations to chemical pollutants and found that the taxonomic and genetic diversities of these populations were much lower than the undisturbed reference communities. Okamura and Aoyama (1994) have investigated the interactive toxic effect of two metals (Cd, Cr) on algal growth and have shown the importance of synergistic effects. Hyne and Wilson (1997) have shown that significant mortality of the early life stages of Australian bass occurs if they are exposed to acid - sulphate soil leachate in presence of aluminium in the receiving estuarine water. (See also Stratton, 1983; Aoyama and Okamura, 1984; Aoyama and Okamura, 1993; Okamura and Aoyama, 1994). Munkittrick *et al* (1991) have reviewed and discussed the relative sensitivity and correlation between Microtox test and three commonly used acute lethality bioassays (rainbow trout, fished minnow, *Daphnia*).

5. EFFECTS OF TOXICANTS (POLLUTANTS) ON BIOLOGICAL SPECIES: STUDIES USING MATHEMATICAL MODELS

From the above literature survey of experimental studies, we note that toxicants emitted in to the environment are harmful to populations living in the habitat. Its study is therefore quite important from the point of view of sustainable growth and biodiversity. In past several decades, mathematical models have become usual tool to analyze and predict the behavior of ecological systems but modelling the effects of toxicants on biological populations in both terrestrial and aquatic ecosystems is relatively new area of research in ecotoxicology. It may be emphasized that most of the studies in past have been experimental and endeavors to understand these phenomena using mathematical models are limited. In recent decades the effect of a single toxicant on various ecosystems have been studied using mathematical models (Wallis, 1975; Hallam and Clark, 1982, Hallam *et al*, 1983a,b; Hallam and Deluna, 1984; DeLuna and Hallam, 1987; Barber *et al*, 1988; Freedman and Shukla, 1991). In particular, Hallam *et al*. (1983a) studied the effect of a toxicant emitted into the environment on a population by assuming that the growth rate of population density depends upon the uptake concentration of the toxicant by this population but they did not consider the effect of environmental toxicant on the carrying capacity of the environment. However, Freedman and Shukla (1991) studied the role of a toxicant on a single species and predator - prey system by considering its effect on both the growth rate of the population as well as its carrying capacity. Huaping and Ma Zhien (1991) studied the effect

of pollutant in a two species competitive system using mathematical model. Chattopadhyay (1996) presented a model to study the effect of toxic substances on a two species competitive system. Further, Shukla and Dubey (1996) proposed and analyzed a non linear model to study the simultaneous effect of two toxicants, one being more toxic than the other, on a biological population. Durrett and Levin (1997) presented a mathematical model for allelopathy in spatially distributed populations. Mukhopadhyay et al (1998) studied the phenomenon of plankton allelopathy using delay differential equations.

Keeping in view, the above brief review of both experimental and modelling studies relevant to effects of toxicants (pollutants) on biological species, the aim of this thesis is to propose new models which break new grounds or illustrate the importance of some new aspects of significant interest and relevant to both new and old phenomena.

6. PROBLEMS STUDIED IN THE THESIS

The non linear models for the following cases are proposed and analyzed in the thesis:

- i). Effect of a toxicant on a biological species, discharged by the species itself in its own environment.
- ii). Effects of two toxicants on a biological species: one toxicant being discharged by species itself and the other toxicant being emitted in to the environment from some external source.
- iii). Effects of primary and secondary toxicants on a biological species.

- iv). Effects of two or more toxicants on a biological species, the toxicants being emitted from external sources.
- v). Effect of a toxicant produced by a plant species on the other competing species: the case of allelopathy.
- vi). Effects of a toxicant on two competing biological species, toxicant being emitted by some external source.
- vii). Effects of a toxicant on two competing biological species, toxicant being produced by one species and affecting both the species.
- viii). Effect of a toxicant on a biological population with a subclass of the total population exhibiting severe symptoms such as reduction in size, deformity, lesion, etc.

7. METHOD OF ANALYSIS

The proposed mathematical models for the various situations, described above, are non - linear. We have used the stability analysis of differential equations to analyze these models. (LaSalle and Lefschetz, 1961; Freedman, 1987; Shukla and Dubey, 1996,1997). In this method, first the existence of positive equilibria is established. The local stability behavior of these equilibria have been studied by either using variational matrix method or using linearisation technique and Lyapunov's functions. The global stability behavior of the equilibria have been studied by using Lyapunov's functions.

The work presented in this thesis, emphasizes the importance of a new area of research in India on modelling of ecological systems stressed by toxicants either discharged by external sources or by the species themselves causing changes in their habitats. (see Shukla and Dubey, 1996; Shukla et al, 1996)

CHAPTER - II

EFFECT OF A TOXICANT ON A BIOLOGICAL SPECIES, DISCHARGED BY ITSELF IN ITS OWN ENVIRONMENT

1. INTRODUCTION

Due to rapid pace of industrialization, caused by various man made projects, one of the most important problems that the modern society faces today is pollution of the environment, affecting the quality of life, health of people, depletion of resources, etc. Both terrestrial and aquatic environments are being deteriorated by discharges of hazardous wastes, poisonous gases, toxic elements such as arsenic, cadmium, cyanide, lead, zinc, etc. threatening the survival of biological species. (Jorgensen, 1956; Nelson, 1970; Patin, 1982; Chung and Miller, 1995a,b). It is therefore, essential to study various effects of pollutants/toxicants on biological species living in a polluted environment.

As pointed out in Chapter I, effects of toxicants/pollutants on biological species using mathematical models have been studied by many investigators (Hallam et al., 1983a,b; Hallam and DeLuna, 1984; DeLuna and hallam, 1987; Freedman and Shukla, 1991; Huaping and Ma, 1991; Shukla and Dubey, 1997). It may be noted that the effects of toxicants, considered in various models, are such that it decreases the growth rate of the biological species as well as its carrying capacity with respect to environment (Freedman and Shukla, 1991; Shukla and Dubey, 1997). The case becomes quite interesting when we consider a situation in which the species

itself produces toxicants in its own environment affecting itself (Rescigno, 1977). This situation is very relevant in the case of human population which pollutes its own habitat affecting not only itself but also other biological species as well.

It may be pointed out here that in the model of Rescigno (1977), the uptake concentration of the toxicant by the biological species is not considered, though, it is this concentration which essentially decreases the growth rate of the species. Therefore, in this chapter, we propose and analyze a non linear mathematical model to study the existence and survival of a biological species under the effect of a toxicant which is being produced in the environment by the species itself. It is assumed that the growth rate of the species decreases as the uptake concentration of toxicant produced by it increases but its carrying capacity decreases due to the presence of toxicant in the environment. It is further assumed that the rate of the production of the toxicant by the species is a function of the biomass density of the biological population and is depleted by some natural degradation factors. It is also assumed that the growth rate of uptake concentration of toxicant is proportional to the density of the species and the environmental concentration of the toxicant. The increase in the uptake concentration of the toxicant is assumed to be the same as the decrease in the concentration of the toxicant in the environment. The stability theory of differential equation (La Salle and Lefschetz, 1961) is used to analyze the model.

We assume that all functions utilized here are sufficiently smooth and that the solution to the initial value problem exists

uniquely and are continuous for all positive values of time.

2. MATHEMATICAL MODEL

We consider a biological species in a habitat which is being polluted by the toxicant which is produced by the species itself. Using the above mentioned considerations and similar arguments as (Freedman and Shukla, 1991), the system is assumed to be governed by following non linear differential equations :

$$\begin{aligned}\frac{dN}{dt} &= \left[r(U) - \frac{r_0 N}{K(T)} \right] N \\ \frac{dT}{dt} &= Q(N) - \delta_0 T - \alpha NT + \pi \nu NU \\ \frac{dU}{dt} &= -\delta_1 U + \alpha NT - \nu NU\end{aligned}\tag{2.1}$$

$$N(0) = N_0 \geq 0, T(0) = T_0 \geq 0, U(0) = cN_0, c \geq 0, 0 \leq \pi \leq 1.$$

Here $N(t)$ is the density of the biological population, $T(t)$ is the concentration of the toxicant in the environment and $U(t)$ is the uptake concentration of toxicant by the population. The constant $\delta_0 > 0$ is the natural washout rate coefficient of $T(t)$, $\alpha > 0$ is the depletion rate coefficient of $T(t)$ due to its uptake by population, $\delta_1 > 0$ is the natural washout rate coefficient of $U(t)$. The coefficient α is a proportionality constant which determines the rate by which the toxicant is uptaken by the species from the environment (i.e. αNT). The constant $\nu > 0$ is the depletion rate coefficient of $U(t)$ due to decay of some members of $N(t)$ and a fraction π of which may re-enter into the environment. The constant

$c \geq 0$ is the proportionality constant determining the measure of initial toxicant concentration in the population at $t = 0$.

It may be noted that in modelling the system (2.1), the growth rate of uptake concentration $U(t)$ is assumed to increase by the same amount as the rate of depletion of the toxicant in the environment due to its uptake by the population.

In our model (2.1), the function, $r(U)$ denotes the growth rate coefficient of the biological population which decreases with U and hence we assume that

$$r(0) = r_0 > 0, \quad \frac{dr}{dU} < 0 \quad \text{for } U > 0 \quad (2.2)$$

The function, $K(T)$ denotes the maximum population density which the environment can support and it also decreases with T and hence we assume that

$$K(0) = K_0 > 0, \quad \frac{dK}{dT} < 0 \quad \text{for } T > 0 \quad (2.3)$$

The function, $Q(N)$, is the rate of discharge of toxicant into the environment by the biological species and is assumed to be an increasing function of N such that,

$$Q(0) = Q_0 \geq 0, \quad Q'(N) > 0 \quad \text{for all } N \geq 0.$$

In our analysis, we consider the following two cases:

Case (i) $Q(N) = \lambda N$ and

Case (ii) $Q(N) = Q_0 + \lambda N$,

where λ is a positive constant denoting the rate of discharge of the toxicant by the biological species with environmental

concentration $T(t)$. The case $Q(N) = Q_0$ has been already studied by Freedman and Shukla (1991).

The first case corresponds to the situation when discharge of toxicant is proportional to the density of the biological population only whereas in the second case it is assumed that the same toxicant is being discharged into the environment with a rate which is linearly related to the density of the biological population.

3. MATHEMATICAL ANALYSIS

3.1 THE CASE WHEN $Q(N) = \lambda N$

In this case, the model (2.1) has two nonnegative equilibria, namely $E_1(0,0,0)$, and $E_2(N^*, T^*, U^*)$. The existence of E_1 is obvious. We shall show the existence of E_2 as follows.

Here N^* , T^* and U^* are the positive solution of the system of equations

$$N = \frac{r(U)K(T)}{r_0} \quad (3.1a)$$

$$T = \frac{\lambda N(\delta_1 + \nu N)}{f(N)} = g(N) \quad (3.1b)$$

$$U = \frac{\lambda \alpha N^2}{f(N)} = h(N) \quad (3.1c)$$

$$\text{where } f(N) = \delta_0 \delta_1 + (\delta_0 \nu + \alpha \delta_1)N + \alpha \nu (1 - \pi)N^2 \quad (3.1d)$$

We note that both T and U increase as λ increases and thus $r(U)$ and $K(T)$ decrease with λ .

$$\text{Let } F(N) = r_0 N - r(h(N))K(g(N)) \quad (3.1e),$$

we then note from (3.1e) that

$$F(0) < 0 \text{ and } F(K_0) > 0.$$

This guarantees the existence of a root of $F(N) = 0$ for $0 < N < K_0$, say N^* . Further, this root will be unique provided

$$F'(N) = r_0 - \left\{ r \frac{dK}{dT} \frac{dg}{dN} + K \frac{dr}{dU} \frac{dh}{dN} \right\} > 0 \quad (3.1f)$$

We note from (2.2) and (2.3) that

$$r'(U) = \frac{dr}{dU} < 0 \text{ and } K'(T) = \frac{dK}{dT} < 0,$$

therefore the condition (3.1f) is satisfied if

$$g'(N) = \frac{dg}{dN} > 0 \text{ and } h'(N) = \frac{dh}{dN} > 0.$$

On computation from (3.1b) and (3.1c), we get that

$$g'(N) = \frac{\lambda}{f^2} \left[\delta_0 \delta_1 \nu N + \delta_0 \nu^2 N^2 + \delta_0 \delta_1 (\delta_1 + \nu N) + \delta_1 \pi \alpha \nu N^2 \right] > 0$$

and

$$h'(N) = \frac{\lambda \alpha N}{f^2} \left[2\delta_0 \delta_1 + (\delta_0 \nu + \alpha \delta_1) N \right] > 0$$

Hence, the condition (3.1f) is automatically satisfied in this case and the uniqueness of N^* is guaranteed without any condition.

Knowing the value of N^* , the values of T^* and U^* can be computed from equations (3.1b) and (3.1c).

3.1.1 STABILITY ANALYSIS

3.1.1 (i) LOCAL STABILITY VIA EIGEN VALUE METHOD AND OSCILLATORY SOLUTION

To study the local stability behavior of the equilibria, we compute the variational matrices corresponding to the equilibria. Let M_i be the variational matrix corresponding to the equilibria E_i , then we have,

$$M_1 = \begin{bmatrix} r_0 & 0 & 0 \\ \lambda & -\delta_0 & 0 \\ 0 & 0 & -\delta_1 \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -\frac{r_0 N^*}{K(T^*)} & \frac{r_0 N^{*2}}{K^2(T^*)} K'(T^*) & r'(U^*) N^* \\ \lambda - (\alpha T^* - \pi \nu U^*) & -(\delta_0 + \alpha N^*) & \pi \nu N^* \\ \alpha T^* - \nu U^* & \alpha N^* & -(\delta_1 + \nu N^*) \end{bmatrix}$$

From M_1 we note that E_1 is a saddle point, unstable locally in N - direction and with stable manifold locally in T - U space.

It can be checked that the eigen values of M_2 have negative real parts (using Routh - Hurwitz criterion). Therefore E_2 is locally asymptotically stable.

The characteristic equation corresponding to M_2 can be written as follows:

$$p(x) = x^3 + bx^2 + cx + d = 0$$

where

$$b = \frac{r_0 N^*}{K(T^*)} + (\delta_0 + \alpha N^*) + (\delta_1 + \nu N^*)$$

$$c = \frac{r_0 N^*}{K(T^*)} + (\delta_0 + \alpha N^*) + (\delta_1 + \nu N^*) + \left\{ \delta_0 \delta_1 + (\alpha \delta_1 + \nu \delta_0) N^* + \right.$$

$$\left. (1 - \pi) \alpha \nu N^{*2} \right\} + \frac{r_0 N^{*2}}{K^2(T^*)} \left\{ -K'(T^*) \right\} \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\}$$

$$+ \left\{ -r'(U^*) \right\} N^* (\alpha T^* - \nu U^*)$$

$$\begin{aligned}
d = & \frac{r_0 N^*}{K(T^*)} \left\{ \delta_0 \delta_1 + (\alpha \delta_1 + \nu \delta_0) N^* + (1 - \pi) \alpha \nu N^{*2} \right\} \\
& + \frac{r_0 N^{*2}}{K^2(T^*)} \left\{ -K'(T^*) \right\} \left[(\delta_1 + \nu N^*) \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\} \right. \\
& \left. + \pi \nu N^* (\alpha T^* - \pi \nu U^*) \right] + \left\{ -r'(U^*) \right\} N^* \\
& \left[\alpha N^* \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\} + (\delta_0 + \alpha N^*) (\alpha T^* - \nu U^*) \right]
\end{aligned}$$

We note that all the coefficients b , c , d are positive.

We know that a cubic polynomial of the above form has one real root and two complex roots (conjugate to each other) provided its discriminant is positive (Dickson, 1976) i.e.

$$\Delta = 18bcd - 4b^3d + b^2c^2 - 4c^3 - 27d^2 > 0$$

Thus the solutions of the model (2.1) will be oscillatory (locally) and settling down to E_2 provided the above condition holds. This result is similar as speculated by Rescigno (1977).

3.1.1 (ii) STABILITY VIA LYAPUNOV'S METHOD

First, we shall study the local stability of E_2 . Linearising the model (2.1) about E_2 and considering

$$N = N^* + n, \quad T = T^* + \tau \quad \text{and} \quad U = U^* + u,$$

where n , τ and u are small perturbations about E_2 , we get the linearised system of equations (2.1) as

$$\frac{dn}{dt} = - \frac{r_0 N^*}{K(T^*)} n + \frac{r_0 N^{*2}}{K^2(T^*)} K'(T^*) \tau + r'(U^*) N^* u$$

$$\frac{d\tau}{dt} = \left[\lambda - (\alpha T^* - \pi \nu U^*) \right] n - (\delta_0 + \alpha N^*) \tau + \pi \nu N^* u$$

$$\frac{du}{dt} = (\alpha T^* - \nu U^*) n + \alpha N^* \tau - (\delta_1 + \nu N^*) u$$

Taking the following positive definite function

$$U(n, \tau, u) = \frac{1}{2N^*} n^2 + \frac{1}{2} \tau^2 + \frac{1}{2} u^2 ,$$

differentiating it with respect to t and writing it along the solution of the above linearised system, we get

$$\begin{aligned} \frac{dU}{dt} = & - \frac{r_0}{K(T^*)} n^2 - (\delta_0 + \alpha N^*) \tau^2 - (\delta_1 + \nu N^*) u^2 \\ & + \left[\frac{r_0 N^*}{K^2(T^*)} K'(T^*) + \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\} \right] n\tau \\ & + \left[r'(U^*) + (\alpha T^* - \nu U^*) \right] nu + (\pi \nu + \alpha) N^* \tau u \end{aligned}$$

writing $\frac{dU}{dt}$ in quadratic form, we have,

$$\begin{aligned} \frac{dU}{dt} = & - \frac{1}{2} a_{11} n^2 + a_{12} n\tau - \frac{1}{2} a_{22} \tau^2 \\ & - \frac{1}{2} a_{11} n^2 + a_{13} nu - \frac{1}{2} a_{33} u^2 \\ & - \frac{1}{2} a_{22} \tau^2 + a_{23} \tau u - \frac{1}{2} a_{33} u^2 \end{aligned}$$

$$\text{where } a_{11} = - \frac{r_0}{K(T^*)}, \quad a_{22} = - (\delta_0 + \alpha N^*), \quad a_{33} = - (\delta_1 + \nu N^*),$$

$$a_{12} = \frac{r_0 N^*}{K^2(T^*)} K'(T^*) + \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\} ,$$

$$a_{13} = r'(U^*) + (\alpha T^* - \nu U^*) \text{ and } a_{23} = (\pi \nu + \alpha) N^*$$

Now, $\frac{dU}{dt}$ will be negative definite, provided

$$a_{12}^2 < a_{11} a_{22} , \quad a_{13}^2 < a_{11} a_{33} , \quad a_{23}^2 < a_{22} a_{33} \text{ which gives in turn,}$$

$$\left[\frac{r_0 N^*}{K^2(T^*)} K'(T^*) + \left\{ \lambda - (\alpha T^* - \pi \nu U^*) \right\} \right]^2 < \frac{r_0}{K(T^*)} (\delta_0 + \alpha N^*)$$

$$\left[r'(U^*) + (\alpha T^* - \nu U^*) \right]^2 < \frac{r_0}{K(T^*)} (\delta_1 + \nu N^*)$$

$$(\pi \nu + \alpha)^2 N^{*2} < (\delta_0 + \alpha N^*) (\delta_1 + \nu N^*) \quad (3.1.1)$$

This shows that under the above conditions U is a Lyapunov's function for the linearised system and hence E_2 is locally asymptotically stable provided the conditions (3.1.1) are satisfied.

In the following theorem we show that E_2 is globally asymptotically stable under certain conditions. To prove this theorem we give the following lemma without proof which establishes a region of attraction for our system (2.1).

LEMMA 3.1 The set

$$\Omega_1 = \left\{ (N, T, U) : 0 \leq N \leq K_0, 0 \leq T + U \leq \frac{\lambda K_0}{\delta} \right\}$$

where $\delta = \min (\delta_0, \delta_1)$

attracts all solutions initiating in the positive octant.

THEOREM 3.1 In addition to the assumptions (2.2) and (2.3), let $r(U)$ and $K(T)$ satisfy in Ω_1 :

$$K_m \leq K(T) \leq K_0, 0 \leq -r'(U) \leq p, 0 \leq -K'(T) \leq q \quad (3.2)$$

for some positive constants K_m , p and q .

Then if the following inequalities hold :

$$\left[\lambda + \frac{r_0 q K_0}{K_m^2} + (\alpha + \pi\nu) \frac{\lambda K_0}{\delta} \right]^2 < \frac{r_0}{K(T^*)} (\delta_0 + \alpha N^*) \quad (3.3a)$$

$$\left[p + (\alpha + \nu) \frac{\lambda K_0}{\delta} \right]^2 < \frac{r_0}{K(T^*)} (\delta_1 + \nu N^*) \quad (3.3b)$$

$$\left[(\pi\nu + \alpha) N^* \right]^2 < (\delta_0 + \alpha N^*) (\delta_1 + \nu N^*) \quad (3.3c)$$

E_2 is globally asymptotically stable in Ω_1 .

It may be relevant to note that when the conditions (3.3) are satisfied, the conditions for local stability i.e. (3.1.1) are also satisfied.

PROOF: We consider the following positive definite function about E_2 ,

$$V(N, T, U) = \left[N - N^* - N^* \ln \frac{N}{N^*} \right] + \frac{1}{2} (T - T^*)^2 + \frac{1}{2} (U - U^*)^2 \quad (3.4a)$$

Differentiating V with respect to t along the solution of (2.1), we get

$$\begin{aligned} \dot{V} = & (N - N^*) \left[r(U) - \frac{r_0 N}{K(T)} \right] + (T - T^*) \left[\lambda N - \delta_0 T - \alpha NT + \pi\nu NU \right] \\ & + (U - U^*) \left[-\delta_1 U + \alpha NT - \nu NU \right] \end{aligned} \quad (3.4b)$$

using (3.1), after a little algebraic manipulation, (3.4b) yields,

$$\begin{aligned} \dot{V} = & - \frac{r_0}{K(T^*)} (N - N^*)^2 - (\delta_0 + \alpha N^*) (T - T^*)^2 - (\delta_1 + \nu N^*) (U - U^*)^2 \\ & + (N - N^*) (T - T^*) \left[-r_0 \eta(T) N + \left\{ \lambda - (\alpha T - \pi\nu U) \right\} \right] \\ & + (N - N^*) (U - U^*) \left[\xi(U) + (\alpha T - \nu U) \right] \\ & + (T - T^*) (U - U^*) \left[(\pi\nu + \alpha) N^* \right] \end{aligned} \quad (3.4c)$$

where

$$\xi(U) = \begin{cases} \frac{r(U) - r(U^*)}{(U - U^*)} , & U \neq U^* \\ r'(U^*) , & U = U^* \end{cases}$$

$$\eta(T) = \begin{cases} \left[\frac{1}{K(T)} - \frac{1}{K(T^*)} \right] / (T - T^*) , & T \neq T^* \\ - \frac{K'(T^*)}{K^2(T^*)} , & T = T^* \end{cases} \quad (3.4d)$$

using (3.4d) and mean value theorem, we get

$$|\xi(U)| \leq p, \quad |\eta(T)| \leq q / K_m^2 \quad (3.4e)$$

\dot{V} can further be written as sum of the quadratics,

$$\begin{aligned} \dot{V} = & -\frac{1}{2} b_{11} (N - N^*)^2 + b_{12} (N - N^*) (T - T^*) - \frac{1}{2} b_{22} (T - T^*)^2 \\ & - \frac{1}{2} b_{11} (N - N^*)^2 + b_{13} (N - N^*) (U - U^*) - \frac{1}{2} b_{33} (U - U^*)^2 \\ & - \frac{1}{2} b_{22} (T - T^*)^2 + b_{23} (T - T^*) (U - U^*) - \frac{1}{2} b_{33} (U - U^*)^2 \end{aligned} \quad (3.4f)$$

where

$$\begin{aligned} b_{11} &= \frac{r_0}{K(T^*)} , \quad b_{22} = (\delta_0 + \alpha N^*) , \quad b_{33} = (\delta_1 + \nu N^*) , \\ b_{12} &= \left[-r_0 \eta(T) N + \left\{ \lambda - (\alpha T - \pi \nu U) \right\} \right] , \\ b_{13} &= \left[\xi(U) + (\alpha T - \nu U) \right] , \quad b_{23} = \left[(\pi \nu + \alpha) N^* \right] \end{aligned} \quad (3.4g)$$

We note from (3.4f) that \dot{V} will be negative definite if the following inequalities hold :

$$b_{12}^2 < b_{11} b_{22} , \quad b_{13}^2 < b_{11} b_{33} , \quad b_{23}^2 < b_{22} b_{33} \quad (3.4h)$$

Which imply (3.3) respectively. Hence V is a Lyapunov function with respect to E_2 whose domain contains the region of attraction Ω_1 , proving the theorem.

3.2 A PARTICULAR QUASI STEADY STATE CASE WHEN $Q(N) = \lambda N$

We discuss here a particular case of the above model (2.1) in which we assume that the environmental and uptake concentrations of the toxicant are under quasi steady state such that the equilibria of concentrations of toxicant are attained with the density of the biological species almost instantaneously. In such a case, we assume

$$\frac{dT}{dt} \approx 0 \quad \text{and} \quad \frac{dU}{dt} \approx 0 \quad \text{for all } t \geq 0.$$

We then have from second and third equations of (2.1)

$$T \approx \frac{\lambda N(\delta_1 + \nu N)}{f(N)} = g(N) \quad \text{and} \quad U \approx \frac{\lambda \alpha N^2}{f(N)} = h(N) \quad (4.1)$$

where $f(N)$, $g(N)$ and $h(N)$ are same as given in (3.1b-d).

In this case the model (2.1) reduces to a one dimensional form of logistic equation as follows with r and K as functions of N through U and T , defined by (4.1),

$$\frac{dN}{dt} = \left[r(U) - \frac{r_0 N}{K(T)} \right] N \quad (4.2)$$

The system (4.2) has only two equilibrium points (0) and (\bar{N}) where \bar{N} is given by

$$r_0 \bar{N} - r(h(\bar{N})) K(g(\bar{N})) = 0 \quad (4.3)$$

which exists uniquely as shown before in section § 3.1.

Using a comparison theorem, it can be noted from (4.2) that

$$\frac{dN}{dt} \leq r_0 \left(1 - \frac{N}{K_0} \right) N$$

This implies that $0 < \bar{N} < K_0$.

Since U and T both increase as λ increases, \bar{N} decreases as λ increases. Further with appropriate choice of $r(U)$ and $K(T)$, the solution of (4.2) may be oscillatory as pointed out in section § 3.1.

It can be proved that (see corresponding result of § 3.4) this equilibrium \bar{N} is globally asymptotically stable provided

$$p_1 < r_0 K_0 q_1 / K_{m1}^2 + \frac{r_0}{K(T(\bar{N}))} \quad (4.4)$$

The above analyses in sections § 3.1 or § 3.2 imply that if the inequalities (3.3) and (4.4) hold, the biological population will settle down to its equilibrium level in which the density of population will be lower than its initial carrying capacity and depends upon the influx and washout rates of toxicants, the influx rate of toxicant being dependent upon the equilibrium population density.

The possibility of oscillatory behavior of the solution (of the linearised system) also does exist in this study as noted by Rescigno (1977).

3.3. THE GENERAL CASE WHEN $Q(N) = Q_0 + \lambda N$

In this case, the following model is obtained from (2.1):

$$\begin{aligned} \frac{dN}{dt} &= \left[r(U) - \frac{r_0 N}{K(T)} \right] N \\ \frac{dT}{dt} &= (Q_0 + \lambda N) - \delta_0 T - \alpha NT + \pi \nu NU \\ \frac{dU}{dt} &= -\delta_1 U + \alpha NT - \nu KU \end{aligned} \quad (5.1)$$

$$N(0) = N_0 \geq 0, \quad T(0) = T_0 \geq 0, \quad U(0) = cN_0, \quad c \geq 0, \quad 0 \leq \pi \leq 1.$$

Here Q_0 may be interpreted as the rate by which the same toxicant is emitted into the atmosphere by some external source independent of species. All the other symbols in the model (5.1) have been defined as earlier.

The model (5.1) has two equilibrium points namely $E_3 = (0, \frac{Q_0}{\delta_0}, 0)$, and $E_4(\tilde{N}, \tilde{T}, \tilde{U})$. The existence of E_3 is obvious. The existence of E_4 follows from the existence of E_2 . \tilde{N} , \tilde{T} and \tilde{U} are positive solutions of the following algebraic equations:

$$N = \frac{r(U)K(T)}{r_0} \quad (5.2a)$$

$$T = \frac{(Q_0 + \lambda N)(\delta_1 + \nu N)}{f(N)} = g_2(N) \quad (5.2b)$$

$$U = \frac{\alpha N(Q_0 + \lambda N)}{f(N)} = h_2(N) \quad (5.2c)$$

where $f(N)$ is the same as defined by (3.1d).

However, in this case, the uniqueness of \tilde{N} requires the following condition :

$$\left\{ \delta_0 \delta_1 + (\alpha \delta_1 + \nu \delta_0) N \right\} \lambda N + (Q_0 + \lambda N) \delta_0 \delta_1 - Q_0 (1 - \pi) \alpha \nu N^2 > 0 \quad (5.2d)$$

3.3.1 STABILITY ANALYSIS

3.3.1 (i) LOCAL STABILITY VIA EIGEN VALUE METHOD AND OSCILLATORY SOLUTION

To study the local stability behavior of the equilibria, we compute the variational matrices corresponding to the equilibria. Let M_i be the variational matrix corresponding to the equilibria E_i , then we have,

$$M_3 = \begin{bmatrix} r_0 & 0 & 0 \\ \lambda - \frac{\alpha Q_0}{\delta_0} & -\delta_0 & 0 \\ \frac{\alpha Q_0}{\delta_0} & 0 & -\delta_1 \end{bmatrix}$$

$$M_4 = \begin{bmatrix} -\frac{r_0 \tilde{N}}{K(\tilde{T})} & \frac{r_0 \tilde{N}^2}{K^2(\tilde{T})} K'(\tilde{T}) & r'(\tilde{U}) \tilde{N} \\ \lambda - (\alpha \tilde{T} - \pi \nu \tilde{U}) & -(\delta_0 + \alpha \tilde{N}) & \pi \nu \tilde{N} \\ \alpha \tilde{T} - \nu \tilde{U} & \alpha \tilde{N} & -(\delta_1 + \nu \tilde{N}) \end{bmatrix}$$

From M_3 we note that E_3 is a saddle point, unstable locally in N - direction and with stable manifold locally in T - U space.

As shown in the case, when $Q(N) = \lambda N$, here also the solutions of the model (5.1) can be shown to be oscillatory (locally) provided one out of the three eigen values of M_4 , is real and negative and other two are complex conjugates of each other with negative real parts.

Therefore, writing the characteristic polynomial corresponding to M_4 we have

$$p_1(x) = x^3 + b_1 x^2 + c_1 x + d_1 = 0 \quad (5.2e)$$

where

$$b_1 = \frac{r_0 \tilde{N}}{K(\tilde{T})} + (\delta_0 + \alpha \tilde{N}) + (\delta_1 + \nu \tilde{N})$$

$$\begin{aligned}
c_1 = & \frac{r_0 \tilde{N}}{K(\tilde{T})} + (\delta_0 + \alpha \tilde{N}) + (\delta_1 + \nu \tilde{N}) + \left\{ \delta_0 \delta_1 + (\alpha \delta_1 + \nu \delta_0) \tilde{N} + \right. \\
& \left. (1 - \pi) \alpha \nu \tilde{N}^2 \right\} + \frac{r_0 \tilde{N}^2}{K^2(\tilde{T})} \left\{ -K'(\tilde{T}) \right\} \left\{ \lambda - (\alpha \tilde{T} - \pi \nu \tilde{U}) \right\} \\
& + \left\{ -r'(\tilde{U}) \right\} \tilde{N} (\alpha \tilde{T} - \nu \tilde{U}) \\
d_1 = & \frac{r_0 \tilde{N}}{K(\tilde{T})} \left\{ \delta_0 \delta_1 + (\alpha \delta_1 + \nu \delta_0) \tilde{N} + (1 - \pi) \alpha \nu \tilde{N}^2 \right\} \\
& + \frac{r_0 \tilde{N}^2}{K^2(\tilde{T})} \left\{ -K'(\tilde{T}) \right\} \left[(\delta_1 + \nu \tilde{N}) \left\{ \lambda - (\alpha \tilde{T} - \pi \nu \tilde{U}) \right\} \right. \\
& \left. + \pi \nu \tilde{N} (\alpha \tilde{T} - \pi \nu \tilde{U}) \right] + \left\{ -r'(\tilde{U}) \right\} \tilde{N} \left[\alpha \tilde{N} \left\{ \lambda - (\alpha \tilde{T} - \pi \nu \tilde{U}) \right\} \right. \\
& \left. + (\delta_0 + \alpha \tilde{N}) (\alpha \tilde{T} - \nu \tilde{U}) \right] \tag{5.2f}
\end{aligned}$$

We note that all the coefficients b_1 , c_1 , d_1 are positive. It can be further checked that the eigen values of M_4 have negative real parts (using Routh - Hurwitz criterion). Therefore E_4 is locally asymptotically stable. We know that a cubic polynomial of the above form has one real root and two complex roots (conjugate to each other) provided its discriminant is positive (Dickson, 1976) i.e.

$$\Delta_1 = 18b_1c_1d_1 - 4b_1^3d_1 + b_1^2c_1^2 - 4c_1^3 - 27d_1^2 > 0 \tag{5.2g}$$

Thus, the solutions of the model (5.1) is oscillatory (locally) provided (5.2g) holds where b_1 , c_1 , d_1 are given by (5.2e).

3.3.1 (ii) STABILITY VIA LYAPUNOV'S METHOD

We first study the local stability of E_4 . As shown in the case, when $Q(N) = \lambda N$, here also the same linearisation technique and method of Lyapunov's function can be used to show that E_4 is locally asymptotically stable provided the following conditions hold

$$\begin{aligned} \left[\frac{r_0 \tilde{N}}{K^2(\tilde{T})} K'(\tilde{T}) + \left\{ \lambda - (\alpha \tilde{T} - \pi \nu \tilde{U}) \right\} \right]^2 &< \frac{r_0}{K(\tilde{T})} (\delta_0 + \alpha \tilde{N}) \\ \left[r'(\tilde{U}) + (\alpha \tilde{T} - \nu \tilde{U}) \right]^2 &< \frac{r_0}{K(\tilde{T})} (\delta_1 + \nu \tilde{N}) \\ (\pi \nu + \alpha)^2 \tilde{N}^2 &< (\delta_0 + \alpha \tilde{N}) (\delta_1 + \nu \tilde{N}) \end{aligned} \quad (5.3)$$

In the following theorem we show that E_4 is globally asymptotically stable. To prove this theorem we state without proof the following lemma which establishes a region of attraction for the system (5.1).

LEMMA 5.1 The set

$$\Omega_2 = \left\{ (N, T, U) : 0 \leq N \leq K_0, 0 \leq T + U \leq \frac{Q_0 + \lambda K_0}{\delta} \right\}$$

where $\delta = \min(\delta_0, \delta_1)$

attracts all solutions initiating in the positive octant.

THEOREM 5.1 Let $r(U)$ and $K(T)$ satisfy (2.2), (2.3) and (3.2) in Ω_2 . Then if the following inequalities hold :

$$\left[\lambda + \frac{r_0 Q K_0}{K_m^2} + (\alpha + \pi \nu) \frac{Q_0 + \lambda K_0}{\delta} \right]^2 < \frac{r_0}{K(T^*)} (\delta_0 + \alpha N^*) \quad (5.4a)$$

$$\left[p + (\alpha + \nu) \frac{Q_0 + \lambda K_0}{\delta} \right]^2 < \frac{r_0}{K(T^*)} (\delta_1 + \nu N^*) \quad (5.4b)$$

$$\left[(\pi\nu + \alpha) \tilde{N} \right]^2 < (\delta_0 + \alpha\tilde{N}) (\delta_1 + \nu\tilde{N}) \quad (5.4c)$$

E_4 is globally asymptotically stable in Ω_2 .

The proof of this theorem is similar to the proof of the theorem (3.1).

3.4 A PARTICULAR QUASI STEADY STATE CASE WHEN $Q(N) = Q_0 + \lambda N$

We discuss here a particular case of the model (5.1) in which we assume quasi steady state for environmental and uptake concentrations of the toxicant such that the equilibria of concentrations of toxicant are attained with the density of the biological species almost instantaneously. In such a case, we assume

$$\frac{dT}{dt} \approx 0 \quad \text{and} \quad \frac{dU}{dt} \approx 0 \quad \text{for all } t \geq 0.$$

We then have from second and third equations of (5.1)

$$T \approx \frac{(Q_0 + \lambda N) (\delta_1 + \nu N)}{f(N)} = g_2(N) \quad \text{and} \\ U \approx \frac{\alpha N (Q_0 + \lambda N)}{f(N)} = h_2(N) \quad (5.5)$$

where $f(N)$, $g_2(N)$ and $h_2(N)$ are same as given in (3.1d), (5.2b,c). In this case the model (5.1) reduces to a one dimensional form of logistic equation as follows with r and K as functions of N through U and T as defined in equation (5.5).

$$\frac{dN}{dt} = \left[r(U) - \frac{r_0 N}{K(T)} \right] N \quad (5.6)$$

Thus, the above system has only two equilibrium points (0) and (\hat{N}) where \hat{N} is given by

$$r_0 \hat{N} - r(h_2(\hat{N})) K(g_2(\hat{N})) = 0 \quad (5.7a)$$

which exists uniquely provided the condition (5.2d) is satisfied.

Using a comparison theorem, it can be noted from (5.6) that

$$\frac{dN}{dt} \leq r_0 \left(1 - \frac{N}{K_0} \right) N \quad (5.7b)$$

This implies that $0 < \hat{N} < K_0$.

Since T and U increase as Q_0 or λ increases. Therefore \hat{N} decreases as Q_0 or λ increases and further if Q_0 or λ becomes very large then \hat{N} may even tend to zero. This implies that the species may not survive for large emission rates.

We can check that $N = 0$ is unstable. To find the behavior of \hat{N} , we proceed as follows:

Consider the following positive definite function about \hat{N}

$$V_1(N) = (N - \hat{N} - \hat{N} \ln \frac{N}{\hat{N}})$$

Differentiating V_1 with respect to t along the solution of the model (5.6), we get

$$\begin{aligned} \frac{dV_1}{dt} &= (N - \hat{N}) \left[r(U(N)) - \frac{r_0 N}{K(T(N))} \right] \\ &= (N - \hat{N}) \left[r(U(N)) - r(U(\hat{N})) - \frac{r_0 N}{K(T(N))} + \frac{r_0 \hat{N}}{K(T(\hat{N}))} \right. \\ &\quad \left. - \frac{r_0 N}{K(T(\hat{N}))} + \frac{r_0 \hat{N}}{K(T(N))} \right] \\ &= (N - \hat{N})^2 \left[\xi_1(N) - r_0 \eta_1(N) - \frac{r_0}{K(T(\hat{N}))} \right] \end{aligned} \quad (5.8a)$$

where

$$\xi_1(N) = \begin{cases} [r(U(N)) - r(U(\hat{N}))]/(N - \hat{N}) & , \quad N \neq \hat{N} \\ \left. \frac{\partial r}{\partial U} \frac{dU}{dN} \right|_{N = \hat{N}} & , \quad N = \hat{N} \end{cases} \quad (5.8b)$$

$$\eta_1(N) = \begin{cases} \frac{\frac{1}{K(T(N))} - \frac{1}{K(T(\hat{N}))}}{N - \hat{N}} & , \quad N \neq \hat{N} \\ - \frac{1}{K^2(T(N))} \left. \frac{\partial K}{\partial T} \frac{dT}{dN} \right|_{N = \hat{N}} & , \quad N = \hat{N} \end{cases} \quad (5.8c)$$

Let $r(U(N))$ and $K(T(N))$ satisfy the following conditions

$$K_{m1} \leq K(T(N)) \leq K_0, \quad 0 \leq - \frac{\partial r}{\partial U} \frac{dU}{dN}(\hat{N}) \leq p_1, \quad 0 \leq - \frac{\partial K}{\partial T} \frac{dT}{dN}(\hat{N}) \leq q_1 \quad (5.8d)$$

for some positive constants K_{m1} , p_1 and q_1 .

From (5.8b-d) and the mean value theorem, we note that

$$|\xi_1(N)| \leq p_1 \text{ and } |\eta_1(N)| \leq q_1/K_{m1}^2 \quad (5.8e)$$

Now $\frac{dV_1}{dt}$ can further be written as

$$\frac{dV_1}{dt} \leq (N - \hat{N})^2 \left[p_1 - r_0 K_0 q_1 / K_{m1}^2 - \frac{r_0}{K(T(\hat{N}))} \right]$$

Thus $\frac{dV_1}{dt}$ will be negative definite provided

$$p_1 < r_0 K_0 q_1 / K_{m1}^2 + \frac{r_0}{K(T(\hat{N}))} \quad (5.9)$$

Hence V_1 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium $N = \hat{N}$ and hence this equilibrium is globally asymptotically stable provided the condition (5.9) is satisfied.

It is further noted that the solution of (5.6) may again be oscillatory for suitable choice of $r(U)$ and $K(T)$.

The analyses in § 3.3 or § 3.4 shows that the population density attains an equilibrium level in this case also and this equilibrium level decreases as the emission rate of the toxicant increases. When Q_0 and λ are very large, the population may be driven to extinction.

4. NUMERICAL EXAMPLE AND DISCUSSION

We give here numerical simulation of the equilibria and the stability conditions for the model (5.1). in (5.1), we assume

$$r(U) = r_0 - \frac{a_1 U}{1 + r_1 U} \quad \text{and} \quad K(T) = K_0 - \frac{b_1 T}{1 + m_1 T} \quad (6.1)$$

where $r_0 = 0.7$, $a_1 = 0.01$, $r_1 = 2.2$,

$K_0 = 5.59$, $b_1 = 1.1$, $m_1 = 1.02$

Now with this choice of b_1 and m_1 , we have $\frac{b_1 T}{1 + m_1 T} < 1$

Since $K_m \leq K(T) \leq K_0$, therefore we can choose K_m as $K_m = 3.5$.

We also note from (6.1) that

$$r'(U) = - \frac{a_1}{(1 + r_1 U)^2} \quad \text{and} \quad K'(T) = - \frac{b_1}{(1 + m_1 T)^2}$$

Therefore p and q can be chosen as 1.0 each.

Choosing $\pi = 0.05$, $Q_0 = 10.0$, $\delta_0 = 14.0$, $\delta_1 = 13.0$, $\lambda = 1.0$, $\nu = 0.03$, $\alpha = 0.02$, the equilibrium values \tilde{N} , \tilde{T} and \tilde{U} are computed as

$$\tilde{N} = 5.027712, \quad \tilde{T} = 1.065758, \quad \tilde{U} = 0.008149.$$

The values of b_1 , c_1 , d_1 and Δ_1 as defined by (5.2f) and (5.2g) are computed.

$$b_1 = 27.951305, c_1 = 205.261490, d_1 = 139.716553$$

$$\text{and } \Delta_1 = 21774.800781$$

which shows that with this choice of parameter values the solution of the system (5.1) is not oscillatory locally. However, for a large value of r_0 , viz., $r_0 = 8.26$ and $K_0 = 10.59$, $K_m = 8.5$ the solutions are computed as

$$\tilde{N} = 9.954492, \tilde{T} = 1.405358, \tilde{U} = 0.021039$$

$$\text{and } b_1 = 35.757523, c_1 = 424.784393, d_1 = 1677.155884,$$

$$\Delta_1 = - 2.356747$$

which show that with this choice, the solution is oscillatory locally.

The conditions for global asymptotic stability of E_4 (5.3a-c) are also satisfied with these parameter values.

Further, we have computed the equilibrium point E_4 for a set of parameters and it has been checked that the conditions for global stability of E_4 viz. (5.3a), (5.3b) and (5.3c) are satisfied. We have named these conditions as 1, 2 and 3. In the following tables, a ' + ' sign indicates that the corresponding condition is satisfied while if no sign appears below the condition, then it indicates that the corresponding condition is not satisfied.

In table (2.1), the variation of equilibrium levels i.e. \tilde{N} , \tilde{T} and \tilde{U} have been listed with respect to the parameter α (the depletion rate coefficient of the environmental concentration of the toxicant $T(t)$ due to its uptake by the biological population).

It is observed that with increasing α , \tilde{N} decreases slightly while \tilde{T} decreases and \tilde{U} increase and all the three conditions are satisfied. But if we further increase α , ($\alpha = 0.1$), \tilde{N} increases whereas \tilde{T} and \tilde{U} follow the same initial pattern. However for this value of α , the third condition (5.3c) is not satisfied.

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

α	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
0.001	5.026454	1.072933	0.000410	+ + +
0.005	5.026715	1.071414	0.002048	+ + +
0.010	5.027051	1.069523	0.004088	+ + +
0.020	5.027712	1.065758	0.008149	+ + +
0.050	5.029727	1.054618	0.020168	+ + +
0.100	5.033144	1.036552	0.039671	+ +

$$\delta_0 = 14.0, \delta_1 = 13.0, \lambda = 1.0, \nu = 0.03$$

Table (2.1)

The same study has been conducted with parameter λ (the coefficient by which the biological population produces toxicant). The results obtained are shown in table (2.2).

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

λ	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
0.01	5.135623	0.712728	0.005565	+ + +
0.05	5.130298	0.727281	0.005673	+ + +
0.10	5.123777	0.745431	0.005807	+ + +
0.50	5.076608	0.889149	0.006864	+ + +
1.00	5.027712	1.065758	0.008149	+ + +
1.50	4.987126	1.239793	0.009404	+ +

$$\delta_0 = 14.0, \delta_1 = 13.0, \alpha = 0.02, \nu = 0.03$$

Table (2.2)

It is noted from table (2.2) that as λ increases \tilde{N} decreases while \tilde{T} and \tilde{U} increase.

In table (2.3), the variations with respect to Q_0 , the emission rate of the toxicant in to the environment from external source, are shown.

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

Q_0	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
1.00	5.253901	0.443381	0.003541	+ + +
5.00	5.133479	0.718553	0.005608	+ + +
10.0	5.027712	1.065758	0.008149	+ + +
20.0	4.895657	1.765918	0.013152	+ + +
30.0	4.816799	2.469928	0.018102	+ + +
40.0	4.764460	3.175857	0.023026	+ + +
50.0	4.727196	3.882878	0.027934	+ + +

$$\delta_0 = 14.0, \delta_1 = 13.0, \alpha = 0.02, \lambda = 1.0, \nu = 0.03$$

Table (2.3)

The table (2.3) shows that as Q_0 increase \tilde{N} decreases but \tilde{T} and \tilde{U} increase.

In table (2.4), the variation of \tilde{N} and \tilde{T} with respect to δ_0 (the natural depletion rate coefficient of $T(t)$) are shown.

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

δ_0	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
12.0	4.987371	1.238657	0.009396	+ +
13.0	5.008258	1.145659	0.008726	+ + +
15.0	5.045885	0.996360	0.007646	+ + +
20.0	5.121373	0.752218	0.005858	+ + +
25.0	5.178271	0.604628	0.004760	+ + +
30.0	5.222743	0.505665	0.004015	+ + +
40.0	5.287850	0.381189	0.003064	+ + +
50.0	5.333271	0.306013	0.002480	+ + +

$$\delta_1 = 13.0, \alpha = 0.02, \lambda = 1.0, \nu = 0.03$$

Table (2.4)

It is noted from table (2.4) that as δ_0 increases, \tilde{N} increases while \tilde{T} decreases.

In table (2.5), the variation of \tilde{N} and \tilde{U} with respect to δ_1 (the natural depletion rate coefficient of the uptake concentration $U(t)$) are shown.

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

δ_1	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
8.0	5.027376	1.065737	0.013147	+ +
10.0	5.027552	1.065748	0.010557	+ + +
12.0	5.027669	1.065755	0.008820	+ + +
15.0	5.027786	1.065762	0.007073	+ + +
20.0	5.027909	1.065770	0.005318	+ + +
25.0	5.027979	1.065774	0.004261	+ + +
30.0	5.028031	1.065777	0.003555	+ + +
40.0	5.028090	1.065781	0.002669	+ + +
50.0	5.028128	1.065783	0.002137	+ + +

$$\delta_0 = 14.0, \alpha = 0.02, \lambda = 1.0, \nu = 0.03$$

Table (2.5)

The table (2.5) shows that as δ_1 increase, \tilde{N} increases while \tilde{U} decreases.

In table (2.6), the variation of \tilde{N} with ν (depletion rate coefficient of $U(t)$ due to decay of some members of the biological population) is shown.

$$K_0 = 5.59, K_m = 3.5, Q_0 = 10.0.$$

ν	\tilde{N}	\tilde{T}	\tilde{U}	1 2 3
0.001	5.027706	1.065753	0.008240	+ + +
0.005	5.027706	1.065754	0.008228	+ + +
0.010	5.027712	1.065755	0.008212	+ + +
0.050	5.027718	1.065761	0.008087	+ + +
0.100	5.027722	1.065768	0.007937	+ + +
0.500	5.027786	1.065820	0.006908	+ +

$$\delta_0 = 14.0, \delta_1 = 13.0, \alpha = 0.02, \lambda = 1.0$$

Table (2.6)

The table (2.6) shows that the effect of ν on \tilde{N} is almost negligible.

5. CONCLUSIONS

In this Chapter, a mathematical model is proposed and analyzed to study the effect of a toxicant on a biological species when the emission of toxicant is caused by various actions of a biological species. The model is relevant to the case of human population. The emission rate of the toxicant is taken to be linearly dependent on the population density of biological species. It has been shown that if the emission rate of the toxicant increases the equilibrium level of the biological population decreases. It has been noted that for large emission rate, the population may be driven to extinction. Further, it is noted that there may exist oscillation in the system for an appropriate choice of the growth rate and carrying capacity functions of the biological species when certain conditions are satisfied.

CHAPTER - III

EFFECTS OF TWO TOXICANTS ON A BIOLOGICAL SPECIES : ONE TOXICANT BEING DISCHARGED BY THE SPECIES ITSELF IN ITS OWN ENVIRONMENT

1. INTRODUCTION

In Chapter II, we have studied the effect of one toxicant on a biological species when the toxicant is discharged by various action of the species itself in its own environment relevant to human population. However, in general, more than one toxicants/ with different toxicities may be emitted in the environment by the actions of the species as well as from some external source, affecting the species. In this Chapter, therefore, we wish to model and analyze the simultaneous effects of two toxicants on a biological species when one toxicant is being discharged by the actions of the species itself (such as household discharges, in case of human population) and the other one being emitted by some external source like exhausts from various industries, road traffic, etc.

In recent years, mathematical models for the effect of a single toxicant on a biological population have been studied (Rescigno, 1977; Hass, 1981; Hallam et al, 1983a,b; Hallam and De Luna, 1984; De Luna and Hallam, 1987; Freedman and Shukla, 1991; Shukla and Dubey, 1996). In particular, Rescigno (1977) proposed a mathematical model to study the effect of a toxicant on a biological species by assuming that the toxicant is being produced

by the species itself. But he has not considered the effect of uptake concentration in the model related to the environmental concentration of the toxicant. Hallam et al. (1983a,b) proposed a mathematical model to study the effect of a toxicant on the growth rate of biological species but they did not consider the effect of the environmental concentration of the toxicant on the carrying capacity of the habitat. Freedman and Shukla (1991), however, have proposed a model to study the effect of a toxin on a single species population and the predator-prey system by assuming that the growth rate of species decreases as the uptake concentration of the toxicant increases while the carrying capacity of the habitat decreases as the environmental concentration of the toxicant increases. They have shown that if the emission rate of the toxicant into the environment increases the equilibrium level of the population decreases, the magnitude of which depends upon the influx and washout rates of the toxicant. We point out here that the simultaneous effects of two toxicants on biological species have not been considered in the above mentioned studies. Shukla and Dubey (1996) proposed and analyzed a mathematical model for the simultaneous effects of two toxicants with different toxicities on a biological population, however, they have assumed that both the toxicants are being emitted from some external source which may not be the case always as the toxicant may be produced by the biological species (see Chapter II).

In this Chapter, therefore, we propose a dynamical model to study the simultaneous effects of two toxicants emitted into the environment on a biological population. It is assumed that out of

the two different toxicants, one is being discharged by the species itself (such as household discharges) and the other is being discharged into the environment by some external source. It is also assumed that the toxicities of the two toxicants are different. The cases of instantaneous spill and constant influx of the toxicant, emitted into the environment by some external source, are considered in the model study.

2. MATHEMATICAL MODEL

We consider a biological population growing logistically in its habitat which is simultaneously affected by two different toxicants, the first toxicant is being emitted by some external source and the second toxicant is discharged by the biological species itself through its various actions (such as household discharges), the rate of emission being proportional to the population density of the biological species. We also consider that one toxicant is more toxic than the other. The environmental concentrations of the toxicants are assumed to decrease due to some natural degradation factors. It is also assumed that the rate of uptake concentration of each of the toxicant by the species is different and is same as the depletion rate of environmental concentration of the respective toxicant which is assumed to be proportional to the density of the species as well as the concentration of the toxicant present in the environment. It is considered that the growth rate of the species decreases as the uptake concentration of each of the toxicant increases where as the carrying capacity of the habitat with respect to the species

decreases with the increase in the concentrations of the two toxicants in the environment. It is assumed that when the biological species is exposed to each of the toxicants at the same concentration and for same duration individually, the growth rate of the species in the more toxic case is smaller than that for the less toxic case. However, when the species is exposed to both the toxicants simultaneously, one of them having the same concentration as before, the growth rate of the species decreases further and this decrease is enhanced as the toxicity and the emission rate of the other toxicant increase. Similar assumptions are also made with respect to the carrying capacity of the habitat (Shukla and Dubey, 1996).

Keeping the above in view, the system is assumed to be governed by the following differential equations (Shukla and Dubey, 1996):

$$\begin{aligned}
 \frac{dN}{dt} &= r(U_1, U_2)N - \frac{r_0 N^2}{K(T_1, T_2)} \\
 \frac{dT_1}{dt} &= Q(t) - \delta_1 T_1 - \alpha_1 T_1 N + \pi_1 \nu_1 N U_1 \\
 \frac{dT_2}{dt} &= \lambda N - \delta_2 T_2 - \alpha_2 T_2 N + \pi_2 \nu_2 N U_2 \\
 \frac{dU_1}{dt} &= -\beta_1 U_1 + \alpha_1 T_1 N - \nu_1 N U_1 \\
 \frac{dU_2}{dt} &= -\beta_2 U_2 + \alpha_2 T_2 N - \nu_2 N U_2
 \end{aligned} \tag{2.1}$$

$$\begin{aligned}
 N(0) \geq 0, \quad T_i(0) \geq 0, \quad U_i(0) \geq c_i N(0), \quad 0 \leq \pi_i \leq 1 \\
 i = 1, 2
 \end{aligned}$$

Here $N(t)$ is the population density of the biological species. $Q(t)$ is the emission rate of the first toxicant into the environment with concentration $T_1(t)$. The positive constant λ represents the rate coefficient of emission of the second toxicant caused by household discharges of the biological species with environmental concentration $T_2(t)$. $U_1(t)$ and $U_2(t)$ are the respective uptake concentrations. δ_i 's are the natural washout rate coefficients of $T_i(t)$, α_i 's are the depletion rate coefficients of $T_i(t)$ due to uptake by the biological population. β_i 's are the natural washout rate coefficients of $U_i(t)$. ν_i 's denote the depletion rate coefficients of $U_i(t)$ due to dying out of some members of the populations and fraction π_i of this re-entering into the environment. c_i 's are constants relating to the initial uptake concentration $U_i(0)$ with the initial population $N(0)$. All the constants taken here are assumed to be positive.

In writing down the model (2.1), it is assumed that the growth rate of uptake concentration $U_i(t)$, i.e. $\alpha_i T_i N$, is same as the depletion rate of the toxicant having environmental concentration T_i .

In the model (2.1), the function $r(U_1, U_2)$ represents the growth rate coefficient of biological species which decreases with the increase of U_1 and U_2 . Hence we take

$$r(0,0) = r_0 > 0, \quad \frac{\partial r}{\partial U_1} < 0, \quad \frac{\partial r}{\partial U_2} < 0 \quad \text{for } U_1 > 0, U_2 > 0 \quad (2.2a)$$

where r_0 is the toxicant independent growth rate coefficient.

Following Shukla and Dubey (1996), we assume that T_2 is more toxic than T_1 , therefore the species when exposed individually to the two toxicants at some concentration $U_c > 0$ during time t , its

growth rate in the more toxic case will be smaller than that for the less toxic case i.e.

$$r(0, U_c) < r(U_c, 0) \quad \text{for } U_c > 0. \quad (2.2b)$$

We also then have

$$r(U_1, U_c) < r(0, U_c) < r(U_c, 0) < r(0, 0) \quad \text{for } U_c > 0, U_1 > 0. \quad (2.2c)$$

Similarly the function $K(T_1, T_2)$, the carrying capacity (i.e. the maximum population density which the environment can support), decreases as T_1 and T_2 increase. Hence we take

$$K(0, 0) = K_0 > 0, \quad K(T_1, T_2) > 0 \quad \text{for } T_1 > 0, T_2 > 0$$

$$\frac{\partial K}{\partial T_1} < 0, \quad \frac{\partial K}{\partial T_2} < 0 \quad \text{for } T_1 > 0, T_2 > 0 \quad (2.3a)$$

where K_0 is the toxicant independent carrying capacity.

As in the case of growth rate, we also have

$$K(T_1, T_c) < K(0, T_c) < K(T_c, 0) < K(0, 0) \quad \text{for } T_c > 0, T_1 > 0 \quad (2.3b)$$

The above model is very relevant to human population polluting its own environment by discharging various toxicants through household and industrial discharges with different toxicities.

3. STABILITY ANALYSIS

In the following, we analyze the model (2.1) for $Q(t) = 0$ and $Q(t) = Q_0$ (a positive constant).

3.1 CASE I : $Q(t) = 0$

This case is applicable when toxicant is emitted at $t = 0$ with concentration T_0 . In this case, the model (2.1) has two nonnegative equilibria, namely $E_1(0, 0, 0, 0, 0)$ and $E_2(\bar{N}, 0, \bar{T}_2, 0, \bar{U}_2)$. The

existence of E_1 is obvious and the existence of E_2 is shown as follows:

EXISTENCE OF E_2 :

Here \bar{N} , \bar{T}_2 and \bar{U}_2 are the positive solution of the system of algebraic equations given below.

$$N = r(0, U_2) K(0, T_2) / r_0 \quad (3.1a)$$

$$T_2 = \frac{\lambda N (\beta_2 + \nu_2 N)}{f_2(N)} = h_{22}(N) \quad (\text{say}) \quad (3.1b)$$

$$U_2 = \frac{\lambda \alpha_2 N^2}{f_2(N)} = g_{22}(N) \quad (\text{say}) \quad (3.1c)$$

where

$$f_2(N) = \beta_2 \delta_2 + (\alpha_2 \beta_2 + \nu_2 \delta_2) N + (1 - \pi_2) \alpha_2 \nu_2 N^2 > 0. \quad (3.1d)$$

Substituting the values of T_2 and U_2 in (3.1a) we get

$$r_0 N = r(0, g_{22}(N)) K(0, h_{22}(N))$$

$$\text{Taking } F_1(N) = r_0 N - r(0, g_{22}(N)) K(0, h_{22}(N)) \quad (3.1f)$$

To show the existence of E_2 , it suffices to show that the equation (3.1f) has a unique positive solution in N .

we note that

$$F_1(0) = -r_0 K_0 < 0$$

$$\text{and } F_1(K_0) = \left\{ r_0 - r(0, g_{22}(K_0)) \right\} K_0 > 0$$

Thus, there exists a \bar{N} in the interval $0 < \bar{N} < K_0$ such that

$$F_1(\bar{N}) = 0.$$

For \bar{N} to be unique, we must have

$$\frac{dF_1}{dN} = r_0 - \left[K(0, h_{22}(N)) \frac{\partial r}{\partial U_2} \frac{dg_{22}}{dN} + r(0, g_{22}(N)) \frac{\partial K}{\partial T_2} \frac{dh_{22}}{dN} \right] > 0. \quad (3.1g)$$

Since $\frac{\partial r}{\partial U_2}$ and $\frac{\partial K}{\partial T_2}$ are negative, the above condition is automatically satisfied if $\frac{dg_{22}}{dN}$ and $\frac{dh_{22}}{dN}$ are positive.

The local stability analysis of the equilibria can be studied by computing the variational matrices corresponding to each equilibrium (Freedman, 1987). Let M_i be the variational matrices corresponding to E_i , $i = 1, 2$. Then we can calculate M_i 's from (2.1) as

$$M_1 = \begin{bmatrix} r_0 & 0 & 0 & 0 & 0 \\ 0 & -\delta_1 & 0 & 0 & 0 \\ \lambda & 0 & -\delta_2 & 0 & 0 \\ 0 & 0 & 0 & -\beta_1 & 0 \\ 0 & 0 & 0 & 0 & -\beta_2 \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -\frac{r_0 \bar{N}}{K(0, \bar{T}_2)} & P_{11} \bar{N} & P_{21} \bar{N} & Q_{11} \bar{N} & Q_{21} \bar{N} \\ 0 & -(\delta_1 + \alpha_1 \bar{N}) & 0 & \pi_1 \nu_1 \bar{N} & 0 \\ G_{21} & 0 & -(\delta_1 + \alpha_1 \bar{N}) & 0 & \pi_2 \nu_2 \bar{N} \\ 0 & \alpha_1 \bar{N} & 0 & -(\beta_1 + \nu_1 \bar{N}) & 0 \\ H_{21} & 0 & \alpha_2 \bar{N} & 0 & -(\beta_2 + \nu_2 \bar{N}) \end{bmatrix}$$

where $P_{i1} = -\frac{r_0 \bar{N}}{K^2(0, \bar{T}_2)} \frac{\partial K}{\partial T_i}(0, \bar{T}_2)$, $Q_{i1} = \frac{\partial r}{\partial U_i}(0, \bar{U}_2)$, $i=1,2$

$$G_{21} = \lambda - (\alpha_2 \bar{T}_2 - \pi_2 \nu_2 \bar{U}_2) \quad \text{and} \quad H_{21} = \alpha_2 \bar{T}_2 - \nu_2 \bar{U}_2 \quad (3.2a)$$

Note that $P_{i1} < 0$, $Q_{i1} < 0$ for $i = 1, 2$

and $G_{21} > 0$, $H_{21} > 0$

also since $0 \leq \pi_2 \leq 1 \Rightarrow \pi_2 \nu_2 \bar{U}_2 \leq \nu_2 \bar{T}_2$

$$\Rightarrow \alpha_2 \bar{T}_2 - \pi_2 \nu_2 \bar{U}_2 \geq \alpha_2 \bar{T}_2 - \nu_2 \bar{U}_2 \quad \text{i.e. } G_{21} > H_{21}.$$

From M_1 , we note that E_1 is a saddle point whose unstable manifold is locally in the N direction and whose stable manifold is locally in T_1 - T_2 - U_1 - U_2 space. In general, from M_2 , we can not visualize the behavior of E_2 . We also note that the Routh - Hurwitz criterion in this case, leads to a very cumbersome calculation. Hence, we use Lyapunov's method (linearization technique) to study the behavior of this equilibrium point. In the following theorem, sufficient conditions have been found under which E_2 is locally asymptotically stable. The proof of this theorem is similar to theorem (3.3) and therefore it is omitted.

THEOREM 3.1 Let the following inequalities hold

$$\left[\frac{r_0 \bar{N}}{K^2(0, \bar{T}_2)} \frac{\partial K}{\partial T_1}(0, \bar{T}_2) \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\delta_1 + \alpha_1 \bar{N}) \quad (3.3a)$$

$$\left[\frac{r_0 \bar{N}}{K^2(0, \bar{T}_2)} \frac{\partial K}{\partial T_2}(0, \bar{T}_2) - \left\{ \lambda - (\alpha_2 \bar{T}_2 - \pi_2 \nu_2 \bar{U}_2) \right\} \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\delta_2 + \alpha_2 \bar{N}) \quad (3.3b)$$

$$\left[\frac{\partial r}{\partial U_1}(0, \bar{U}_2) \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\beta_1 + \nu_1 \bar{N}) \quad (3.3c)$$

$$\left[\frac{\partial r}{\partial U_2}(0, \bar{U}_2) + (\alpha_2 \bar{T}_2 - \nu_2 \bar{U}_2) \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\beta_2 + \nu_2 \bar{N}) \quad (3.3d)$$

$$(\pi_1 \nu_1 + \alpha_1)^2 \bar{N}^2 < (\delta_1 + \alpha_1 \bar{N}) (\beta_1 + \nu_1 \bar{N}) \quad (3.3e)$$

$$(\pi_2 \nu_2 + \alpha_2)^2 \bar{N}^2 < (\delta_2 + \alpha_2 \bar{N}) (\beta_2 + \nu_2 \bar{N}) \quad (3.3f)$$

then E_2 is locally asymptotically stable.

Now to show that E_2 is globally asymptotically stable, we first need a lemma which establishes the region of attraction for the system (2.1).

LEMMA 3.1 The set

$$\Omega_1 = \left\{ (N, T_1, T_2, U_1, U_2) : 0 \leq N \leq K_0, 0 \leq T_2 + U_2 \leq \frac{\lambda K_0}{\delta_{20}}, \right. \\ \left. T_1 = 0, U_1 = 0 \right\} \text{ where } \delta_{20} = \min(\delta_2, \beta_2)$$

is a region of attraction for all solutions initiating in the positive orthant. The proof of this Lemma is similar to Lemma (3.2) given later and hence omitted here.

THEOREM 3.2 In addition to the assumptions (2.2) and (2.3), let $r(U_1, U_2)$ and $K(T_1, T_2)$ satisfy the following conditions in Ω_1 ,

$$K_m \leq K(T_1, T_2) \leq K_0, 0 \leq -\frac{\partial r}{\partial U_1}(0, U_2) \leq \rho_{10}, 0 \leq -\frac{\partial r}{\partial U_2}(0, U_2) \leq \rho_{20}$$

$$0 \leq -\frac{\partial K}{\partial T_1}(0, T_2) \leq k_{10}, 0 \leq -\frac{\partial K}{\partial T_2}(0, T_2) \leq k_{20} \quad (3.4)$$

for some positive constants $K_m, \rho_{10}, \rho_{20}, k_{10}, k_{20}$.

Then if the following inequalities hold

$$\left[\frac{r_0 k_{10} K_0}{K_m^2} \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\delta_1 + \alpha_1 \bar{N}) \quad (3.5a)$$

$$\left[\frac{r_0 k_{20} K_0}{K_m^2} + \lambda + (\alpha_2 + \pi_2 \nu_2) \frac{\lambda K_0}{\delta_{20}} \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\delta_2 + \alpha_2 \bar{N}) \quad (3.5b)$$

$$\rho_{10}^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\beta_1 + \nu_1 \bar{N}) \quad (3.5c)$$

$$\left[\rho_{20} + (\alpha_2 + \nu_2) \frac{\lambda K_0}{\delta_{20}} \right]^2 < \frac{1}{2} \frac{r_0}{K(0, \bar{T}_2)} (\beta_2 + \nu_2 \bar{N}) \quad (3.5d)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) \bar{N} \right]^2 < (\delta_1 + \alpha_1 \bar{N}) (\beta_1 + \nu_1 \bar{N}) \quad (3.5e)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) \bar{N} \right]^2 < (\delta_2 + \alpha_2 \bar{N}) (\beta_2 + \nu_2 \bar{N}) \quad (3.5f)$$

E_2 is globally asymptotically stable with respect to all solutions initiating in the positive orthant. The proof of this theorem is similar to theorem (3.4).

The above theorems imply that in the case of instantaneous spill of the toxicant, the population will settle down to a lower equilibrium level than its initial carrying capacity, the magnitude of which will depend upon the toxicity, emission and washout rate of the second toxicant (emitted by the population itself) as well as on the discharge rate coefficient λ by which it is produced. Thus, in this case eventually the equilibrium level of the biological population is affected by only the toxicant, namely the second one, produced by the species itself.

3.2 CASE II : $Q(t) = Q_0 > 0$ (A CONSTANT)

In this case, the model (2.1) has two nonnegative equilibria, namely $E_3(0, Q_0/\delta_1, 0, 0, 0)$ and $E_4(N^*, T_1^*, T_2^*, U_1^*, U_2^*)$. The existence of E_3 is obvious. We show the existence of E_4 as follows:

Here N^*, T_1^*, T_2^*, U_1^* and U_2^* are the positive solution of the system of algebraic equations given below.

$$N = r(U_1, U_2) K(T_1, T_2) / r_0 \quad (3.6a)$$

$$T_1 = \frac{Q_0 (\beta_1 + \nu_1 N)}{f_1(N)} = h_{21}(N) \quad (\text{say}) \quad (3.6b)$$

$$T_2 = \frac{\lambda N (\beta_2 + \nu_2 N)}{f_2(N)} = h_{22}(N) \quad (\text{say}) \quad (3.6c)$$

$$U_1 = \frac{Q_0 \alpha_1 N}{f_1(N)} = g_{21}(N) \quad (\text{say}) \quad (3.6d)$$

$$U_2 = \frac{\lambda \alpha_2 N^2}{f_2(N)} = g_{22}(N) \quad (\text{say}) \quad (3.6e)$$

where

$$f_1(N) = \beta_1 \delta_1 + (\alpha_1 \beta_1 + \nu_1 \delta_1) N + (1 - \pi_1) \alpha_1 \nu_1 N^2 > 0. \quad (3.6f)$$

and $f_2(N)$ is same as defined by (3.1d).

We note here that T_1 , T_2 , U_1 and U_2 increase as Q_0 or λ increases correspondingly. Thus $r(U_1, U_2)$ and $K(T_1, T_2)$ decrease as Q_0 or λ increases.

Substituting the values of T_1 , T_2 , U_1 , U_2 in (3.6a) we get

$$r_0 N = r(g_{21}(N), g_{22}(N)) K(h_{21}(N), h_{22}(N))$$

$$\text{Let } F_2(N) = r_0 N - r(g_{21}(N), g_{22}(N)) K(h_{21}(N), h_{22}(N)) \quad (3.6g)$$

To show the existence of E_4 , it suffices to show that equation (3.6g) has a unique positive solution in N . We note that

$$F_2(0) = -r_0 K(Q_0/\delta_1, 0) < 0 \quad \text{and}$$

$$F_2(K_0) = r_0 K_0 - r(g_{21}(K_0), g_{22}(K_0)) K(h_{21}(K_0), h_{22}(K_0)) > 0$$

Thus, there exists a N^* in the interval $0 < N^* < K_0$ such that

$$F_2(N^*) = 0.$$

For N^* to be unique, we must have

$$\begin{aligned} \frac{dF_2}{dN} = & r_0 - K(h_{21}(N), h_{22}(N)) \left[\frac{\partial r}{\partial U_1} \frac{dg_{21}}{dN} + \frac{\partial r}{\partial U_2} \frac{dg_{22}}{dN} \right] \\ & - r(g_{21}(N), g_{22}(N)) \left[\frac{\partial K}{\partial T_1} \frac{dh_{21}}{dN} + \frac{\partial K}{\partial T_2} \frac{dh_{22}}{dN} \right] > 0. \end{aligned} \quad (3.6h)$$

Since $\frac{\partial r}{\partial U_1}$, $\frac{\partial r}{\partial U_2}$, $\frac{\partial K}{\partial T_1}$ and $\frac{\partial K}{\partial T_2}$ are negative (from equations (2.2a,b)), the above condition (3.6h) is automatically satisfied if $\frac{dg_{21}}{dN}$, $\frac{dg_{22}}{dN}$, $\frac{dh_{21}}{dN}$ and $\frac{dh_{22}}{dN}$ are positive.

In particular, when only T_1 affects the population and $T_2 = U_2 = 0$ (also $\lambda = 0$), then correspondingly we have from (3.6g)

$$F_{21}(N) = r_0 N - r(h_{21}(N), 0) K(g_{21}(N), 0) \quad (3.7a)$$

and there exists a unique N_1^* in the interval $0 < N_1^* < K_0$ iff the following inequality holds

$$\frac{dF_{21}}{dN} = r_0 - K(g_{21}(N), 0) \frac{\partial r}{\partial U_1} \frac{dh_{21}}{dN} - r(h_{21}(N), 0) \frac{\partial K}{\partial T_1} \frac{dg_{21}}{dN} > 0 \quad (3.7b)$$

Similarly when only T_2 affects the population and $T_1 = U_1 = 0$, we have

$$F_{22}(N) = r_0 N - r(0, h_{22}(N)) K(0, g_{22}(N)) \quad (3.8a)$$

and there exists a unique N_2^* in the interval $0 < N_2^* < K_0$ iff the following inequality holds

$$\frac{dF_{22}}{dN} = r_0 - K(0, g_{22}(N)) \frac{\partial r}{\partial U_2} \frac{dh_{22}}{dN} - r(0, h_{22}(N)) \frac{\partial K}{\partial T_2} \frac{dg_{22}}{dN} > 0 \quad (3.8b)$$

In the case, when no toxicant is present in the environment i.e. $T_1 = T_2 = U_1 = U_2 = 0$, then it is clear from (3.6g) that

$$F_{20}(N) = r_0 N - r_0 K_0 \quad (3.9)$$

and $F_{20}(N) = 0$ has a unique root $N_0^* = K_0$.

Since T_2 is more toxic than T_1 , from (2.2), (2.3), (3.6a), (3.7a) and (3.8a) we note that

$$F_2(N) > F_{21}(N) > F_{22}(N) > F_{20}(N) = r_0(N - K_0) \quad (3.10a)$$

for $h_{21}(N) = h_{22}(N) = U_c > 0$ and $g_{21}(N) = g_{22}(N) = T_c > 0$

Thus we have [see fig.1],

$$N^* < N_2^* < N_1^* < N_0^* = K_0 \quad (3.10b)$$

From the above analysis, it follows that when each of the toxicants affects the biological population individually, the equilibrium level of the population is less in the more toxic case but when both the toxicants affect the population simultaneously the equilibrium density decreases further, the amount of decrease being dependent on their toxicity, emission and washout rates.

Now to study the stability behavior of E_3 and E_4 , we compute the variational matrices M_3 and M_4 corresponding to E_3 and E_4 as follows :

$$M_3 = \begin{bmatrix} r_0 & 0 & 0 & 0 & 0 \\ -\frac{\alpha_1 Q_0}{\delta_1} & -\delta_1 & 0 & 0 & 0 \\ \lambda & 0 & -\delta_2 & 0 & 0 \\ \frac{\alpha_1 Q_0}{\delta_1} & 0 & 0 & -\beta_1 & 0 \\ 0 & 0 & 0 & 0 & -\beta_2 \end{bmatrix}$$

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$$F_2(N) > F_{21}(N) > F_{22}(N) > F_{20}(N)$$

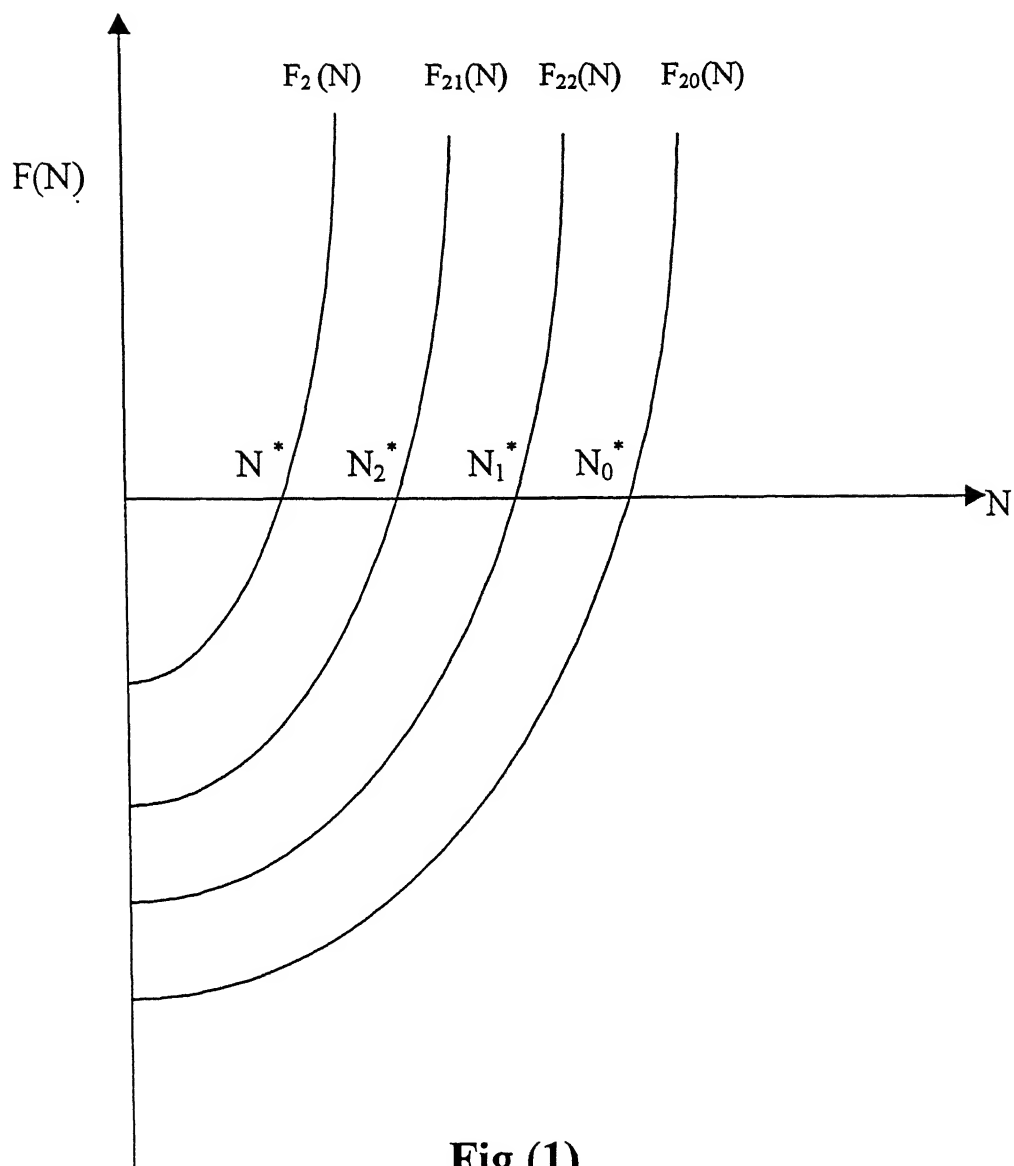


Fig (1)

$$M_4 = \begin{bmatrix} -\frac{r_0 N^*}{K(T_1^*, T_2^*)} & P_{12} N^* & P_{22} N^* & Q_{12} N^* & Q_{22} N^* \\ G_{11} & -\delta_1 - \alpha_1 N^* & 0 & \pi_1 \nu_1 N^* & 0 \\ \lambda - G_{22} & 0 & -\delta_2 - \alpha_2 N^* & 0 & \pi_2 \nu_2 N^* \\ H_{11} & \alpha_1 N^* & 0 & -\beta_1 - \nu_1 N^* & 0 \\ H_{22} & 0 & \alpha_2 N^* & 0 & -\beta_2 - \nu_2 N^* \end{bmatrix}$$

where

$$P_{i2} = \frac{r_0 N^*}{K^2(T_1^*, T_2^*)} \frac{\partial K}{\partial T_i}(T_1^*, T_2^*), \quad Q_{i2} = \frac{\partial r}{\partial U_i}(U_1^*, U_2^*),$$

$$G_{ii} = \alpha_i T_i^* - \pi_i \nu_i U_i^*, \quad H_{ii} = \alpha_i T_i^* - \nu_i U_i^* \quad \text{for } i = 1, 2 \quad (3.11)$$

From M_3 , we note that E_3 is a saddle point with stable manifold locally in the T_1 - T_2 - U_1 - U_2 space and unstable manifold locally in the N direction.

Since it is not obvious to study the behavior of E_4 from M_4 , we use Lyapunov's method to study the stability behavior of E_4 . In the following theorem, we find sufficient conditions under which E_4 is locally asymptotically stable.

THEOREM 3.3 Let the following inequalities hold

$$\left[\frac{r_0 N^*}{K^2(T_1^*, T_2^*)} \frac{\partial K}{\partial T_1}(T_1^*, T_2^*) - \alpha_1 T_1^* + \pi_1 \nu_1 U_1^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\delta_1 + \alpha_1 N^*) \quad (3.12a)$$

$$\left[\frac{r_0 N^*}{K^2(T_1^*, T_2^*)} \frac{\partial K}{\partial T_2}(T_1^*, T_2^*) + \lambda - \alpha_2 T_2^* + \pi_2 \nu_2 U_2^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\delta_2 + \alpha_2 N^*) \quad (3.12b)$$

$$\left[\frac{\partial r(U_1^*, U_2^*)}{\partial U_1} + \alpha_1 T_1^* - \nu_1 U_1^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\beta_1 + \nu_1 N^*) \quad (3.12c)$$

$$\left[\frac{\partial r(U_1^*, U_2^*)}{\partial U_2} + \alpha_2 T_2^* - \nu_2 U_2^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\beta_2 + \nu_2 N^*) \quad (3.12d)$$

$$\left[\pi_1 \nu_1 + \alpha_1 \right]^2 N^{*2} < (\delta_1 + \alpha_1 N^*) (\beta_1 + \nu_1 N^*) \quad (3.12e)$$

$$\left[\pi_2 \nu_2 + \alpha_2 \right]^2 N^{*2} < (\delta_2 + \alpha_2 N^*) (\beta_2 + \nu_2 N^*) \quad (3.12f)$$

Then E_4 is locally asymptotically stable.

PROOF: Linearizing the system (2.1) about E_4 and assuming

$$N = N^* + n, \quad T_1 = T_1^* + \tau_1, \quad T_2 = T_2^* + \tau_2, \quad U_1 = U_1^* + u_1$$

and $U_2 = U_2^* + u_2$ where n, τ_1, τ_2, u_1 and u_2 are small perturbations around E_4 . We get the following linearized system of (2.1)

$$\dot{n} = N^* \left[- \frac{r_0}{K(T_1^*, T_2^*)} n + P_{12} \tau_1 + P_{22} \tau_2 + Q_{12} u_1 + Q_{22} u_2 \right]$$

$$\dot{\tau}_1 = -G_{11} n - (\delta_1 + \alpha_1 N^*) \tau_1 + \pi_1 \nu_1 N^* u_1$$

$$\dot{\tau}_2 = (\lambda - G_{22}) n - (\delta_2 + \alpha_2 N^*) \tau_2 + \pi_2 \nu_2 N^* u_2$$

$$\dot{u}_1 = H_{11} n + \alpha_1 N^* \tau_1 - (\beta_1 + \nu_1 N^*) u_1$$

$$\dot{u}_2 = H_{22} n + \alpha_2 N^* \tau_2 - (\beta_2 + \nu_2 N^*) u_2 \quad (3.13a)$$

Now consider the following positive definite function

$$V = \frac{1}{2} n^2 + \frac{1}{2} \tau_1^2 + \frac{1}{2} \tau_2^2 + \frac{1}{2} u_1^2 + \frac{1}{2} u_2^2 \quad (3.13b)$$

Then $\dot{V} = n\dot{n} + \tau_1\dot{\tau}_1 + \tau_2\dot{\tau}_2 + u_1\dot{u}_1 + u_2\dot{u}_2$

substituting values of \dot{n} , $\dot{\tau}_1$, $\dot{\tau}_2$, \dot{u}_1 and \dot{u}_2 from (3.13a) in to equation (3.13b) and with a little algebraic manipulation, we get

$$\begin{aligned}\dot{V} = & -\frac{1}{2} a_{11} n^2 + a_{12} n\tau_1 - \frac{1}{2} a_{22} \tau_1^2 \\ & - \frac{1}{2} a_{11} n^2 + a_{13} n\tau_2 - \frac{1}{2} a_{33} \tau_2^2 \\ & - \frac{1}{2} a_{11} n^2 + a_{14} nu_1 - \frac{1}{2} a_{44} u_1^2 \\ & - \frac{1}{2} a_{11} n^2 + a_{15} nu_2 - \frac{1}{2} a_{55} u_2^2 \\ & - \frac{1}{2} a_{22} \tau_1^2 + a_{24} \tau_1 u_1 - \frac{1}{2} a_{44} u_1^2 \\ & - \frac{1}{2} a_{33} \tau_2^2 + a_{35} \tau_2 u_2 - \frac{1}{2} a_{55} u_2^2\end{aligned}\quad (3.13c)$$

where $a_{11} = \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)}$, $a_{22} = (\delta_1 + \alpha_1 N^*)$, $a_{33} = (\delta_2 + \alpha_2 N^*)$,

$a_{44} = (\beta_1 + \nu_1 N^*)$, $a_{55} = (\beta_2 + \nu_2 N^*)$,

$a_{12} = P_{12} - G_{11} = \frac{r_0 N^*}{K^2(T_1^*, T_2^*)} \frac{\partial K(T_1^*, T_2^*)}{\partial T_1} - \alpha_1 T_1^* + \pi_1 \nu_1 U_1^*$,

$a_{13} = P_{22} + \lambda - G_{22} = \frac{r_0 N^*}{K^2(T_1^*, T_2^*)} \frac{\partial K(T_1^*, T_2^*)}{\partial T_2} + \lambda - \alpha_2 T_2^* + \pi_2 \nu_2 U_2^*$,

$a_{14} = Q_{12} + H_{11} = \frac{\partial r(U_1^*, U_2^*)}{\partial U_1} + \alpha_1 T_1^* - \nu_1 U_1^*$,

$a_{15} = Q_{22} + H_{22} = \frac{\partial r(U_1^*, U_2^*)}{\partial U_2} + \alpha_2 T_2^* - \nu_2 U_2^*$,

$a_{24} = (\pi_1 \nu_1 + \alpha_1) N^*$ and $a_{35} = (\pi_2 \nu_2 + \alpha_2) N^*$ (3.13d)

From (3.13c) and (3.13d) we note that \dot{V} will be negative definite provided

$$\begin{aligned} a_{12}^2 < a_{11}a_{22} , \quad a_{13}^2 < a_{11}a_{33} , \quad a_{14}^2 < a_{11}a_{44} , \quad a_{15}^2 < a_{11}a_{55} , \\ a_{24}^2 < a_{22}a_{44} , \quad a_{35}^2 < a_{33}a_{55} , \end{aligned} \quad (3.13e)$$

The conditions (3.13e) , in view of (3.13d) respectively give the conditions (3.12).

This shows that under the conditions (3.13e) \dot{V} is negative definite showing that V is a Lyapunov's function for the linearized system and hence the proof of the theorem (3.3) follows.

Now to show that E_4 is globally asymptotically stable, we first need a lemma which establishes the region of attraction for the system (2.1).

LEMMA 3.2 The set

$$\Omega_2 = \left\{ (N, T_1, T_2, U_1, U_2) : 0 \leq N \leq K_0, 0 \leq T_1 + U_1 \leq \frac{Q_0}{\delta_{10}}, \right. \\ \left. 0 \leq T_2 + U_2 \leq \frac{\lambda K_0}{\delta_{20}} \right\}$$

where $\delta_{10} = \min(\delta_1, \beta_1)$ and $\delta_{20} = \min(\delta_2, \beta_2)$

is a region of attraction for all solutions initiating in the positive orthant.

PROOF: From (2.1) we have

$$\begin{aligned} \frac{dN}{dt} &= r(U_1, U_2)N - \frac{r_0 N^2}{K(T_1, T_2)} \\ &\leq r_0 N - \frac{r_0 N^2}{K_0} \end{aligned}$$

hence $\limsup_{t \rightarrow \infty} N(t) = K_0$

We also have

$$\begin{aligned} \frac{dT_1}{dt} + \frac{dU_1}{dt} &= Q_0 - \delta_1 T_1 - \beta_1 U_1 - (1 - \pi_1) \nu_1 N U_1 \\ &\leq Q_0 - \delta_{10} (T_1 + U_1) \quad \text{where } \delta_{10} = \min (\delta_1, \beta_1) \end{aligned}$$

This implies that

$$\begin{aligned} \limsup_{t \rightarrow \infty} [T_1(t) + U_1(t)] &= \frac{Q_0}{\delta_{10}} \\ \text{similarly } \limsup_{t \rightarrow \infty} [T_2(t) + U_2(t)] &= \frac{\lambda K_0}{\delta_{20}} \end{aligned}$$

Hence the proof of the lemma.

THEOREM 3.4 In addition to the assumptions (2.2) and (2.3), let $r(U_1, U_2)$ and $K(T_1, T_2)$ satisfy the following conditions in Ω_2 ,

$$K_m \leq K(T_1, T_2) \leq K_0, \quad 0 \leq -\frac{\partial r}{\partial U_1}(U_1, U_2) \leq \rho_1, \quad 0 \leq -\frac{\partial r}{\partial U_2}(U_1, U_2) \leq \rho_2$$

$$0 \leq -\frac{\partial K}{\partial T_1}(T_1, T_2) \leq k_1, \quad 0 \leq -\frac{\partial K}{\partial T_2}(T_1, T_2) \leq k_2 \quad (3.14)$$

for some positive constants $K_m, \rho_1, \rho_2, k_1, k_2$.

Then if the following inequalities hold

$$\left[\frac{r_0 k_1 K_0}{K_m^2} + (\alpha_1 + \pi_1 \nu_1) \frac{Q_0}{\delta_{10}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\delta_1 + \alpha_1 N^*) \quad (3.15a)$$

$$\left[\frac{r_0 k_2 K_0}{K_m^2} + \lambda + (\alpha_2 + \pi_2 \nu_2) \frac{\lambda K_0}{\delta_{20}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\delta_2 + \alpha_2 N^*) \quad (3.15b)$$

$$\left[\rho_1 + (\alpha_1 + \nu_1) \frac{Q_0}{\delta_{10}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\beta_1 + \nu_1 N^*) \quad (3.15c)$$

$$\left[\rho_2 + (\alpha_2 + \nu_2) \frac{\lambda K_0}{\delta_{20}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)} (\beta_2 + \nu_2 N^*) \quad (3.15d)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N^* \right]^2 < (\delta_1 + \alpha_1 N^*) (\beta_1 + \nu_1 N^*) \quad (3.15e)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N^* \right]^2 < (\delta_2 + \alpha_2 N^*) (\beta_2 + \nu_2 N^*) \quad (3.15f)$$

E_4 is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

PROOF:

We consider the following positive definite function about E_4 ,

$$\begin{aligned} V_1(N, T_1, T_2, U_1, U_2) = & (N - N^* - N^* \ln \frac{N}{N^*}) + \frac{1}{2} (T_1 - T_1^*)^2 \\ & + \frac{1}{2} (T_2 - T_2^*)^2 + \frac{1}{2} (U_1 - U_1^*)^2 + \frac{1}{2} (U_2 - U_2^*)^2 \end{aligned}$$

Differentiating V_1 with respect to t along the solution of the model (2.1), we get

$$\begin{aligned} \frac{dV_1}{dt} = & (N - N^*) \left[r(U_1, U_2) - \frac{r_0 N}{K(T_1, T_2)} \right] \\ & + (T_1 - T_1^*) \left[Q_0 - \delta_1 T_1 - \alpha_1 T_1 N + \pi_1 \nu_1 N U_1 \right] \\ & + (T_2 - T_2^*) \left[\lambda N - \delta_2 T_2 - \alpha_2 T_2 N + \pi_2 \nu_2 N U_2 \right] \\ & + (U_1 - U_1^*) \left[-\beta_1 U_1 + \alpha_1 T_1 N - \nu_1 N U_1 \right] \\ & + (U_2 - U_2^*) \left[-\beta_2 U_2 + \alpha_2 T_2 N - \nu_2 N U_2 \right] \end{aligned} \quad (3.16a)$$

Using (3.6) and simplifying, we get

$$\begin{aligned}
\frac{dv_1}{dt} = & - \frac{r_0}{K(T_1^*, T_2^*)} (N - N^*)^2 - (\delta_1 + \alpha_1 N^*) (T_1 - T_1^*)^2 \\
& - (\delta_2 + \alpha_2 N^*) (T_2 - T_2^*)^2 - (\beta_1 + \nu_1 N^*) (U_1 - U_1^*)^2 \\
& - (\beta_2 + \nu_2 N^*) (U_2 - U_2^*)^2 \\
& - (N - N^*) (T_1 - T_1^*) [r_0^N \eta_1(T_1, T_2) + \alpha_1 T_1 - \pi_1 \nu_1 U_1] \\
& - (N - N^*) (T_2 - T_2^*) [r_0^N \eta_2(T_1^*, T_2) - \lambda + \alpha_2 T_2 - \pi_2 \nu_2 U_2] \\
& + (N - N^*) (U_1 - U_1^*) [\xi_1(U_1, U_2) + \alpha_1 T_1 - \nu_1 U_1] \\
& + (N - N^*) (U_2 - U_2^*) [\xi_2(U_1^*, U_2) + \alpha_2 T_2 - \nu_2 U_2] \\
& + (T_1 - T_1^*) (U_1 - U_1^*) [\pi_1 \nu_1 N^* + \alpha_1 N^*] \\
& + (T_2 - T_2^*) (U_2 - U_2^*) [\pi_2 \nu_2 N^* + \alpha_2 N^*]
\end{aligned} \tag{3.16b}$$

where

$$\xi_1(U_1, U_2) = \begin{cases} [r(U_1, U_2) - r(U_1^*, U_2)] / (U_1 - U_1^*), & U_1 \neq U_1^* \\ \frac{\partial r}{\partial U_1}(U_1, U_2), & U_1 = U_1^* \end{cases} \tag{3.17a}$$

$$\xi_2(U_1^*, U_2) = \begin{cases} [r(U_1^*, U_2) - r(U_1^*, U_2^*)] / (U_2 - U_2^*), & U_2 \neq U_2^* \\ \frac{\partial r}{\partial U_2}(U_1^*, U_2), & U_2 = U_2^* \end{cases} \tag{3.17b}$$

$$\eta_1(T_1, T_2) = \begin{cases} \left[\frac{1}{K(T_1, T_2)} - \frac{1}{K(T_1^*, T_2)} \right] / (T_1 - T_1^*), & T_1 \neq T_1^* \\ - \frac{1}{K^2(T_1^*, T_2)} \frac{\partial K}{\partial T_1}(T_1^*, T_2), & T_1 = T_1^* \end{cases} \tag{3.17c}$$

$$\begin{aligned}
a_{15} &= \xi_2(U_1^*, U_2) + \alpha_2 T_2 - \nu_2 U_2, \\
a_{24} &= \pi_1 \nu_1 N^* + \alpha_1 N^*, \quad a_{35} = \pi_2 \nu_2 N^* + \alpha_2 N^*
\end{aligned} \tag{3.20}$$

The sufficient conditions for $\frac{dV_1}{dt}$ to be negative definite are:

$$a_{12}^2 < a_{11}a_{22} \tag{3.21a}$$

$$a_{13}^2 < a_{11}a_{33} \tag{3.21b}$$

$$a_{14}^2 < a_{11}a_{44} \tag{3.21c}$$

$$a_{15}^2 < a_{11}a_{55} \tag{3.21d}$$

$$a_{24}^2 < a_{22}a_{44} \tag{3.21e}$$

$$a_{35}^2 < a_{33}a_{55} \tag{3.21f}$$

We note that (3.21a,b,c,d,e,f) \Rightarrow (3.15a,b,c,d,e,f) respectively. Hence V_1 is a Lyapunov function (La Salle and Lefschetz, 1961) with respect to E_4 whose domain contains the region of attraction Ω_2 , proving the theorem.

3.3 A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANTS

We assume that the dynamics of the environmental as well as uptake concentrations of both the toxicants are very fast so that their equilibria are attained with the density of the biological species almost instantaneously. In such a case, we assume :

$$\frac{dT_i}{dt} \approx 0 \quad \text{and} \quad \frac{dU_i}{dt} \approx 0 \quad \text{for all } t \geq 0 \text{ and for } i = 1, 2.$$

From last four equations of (2.1), we then have

$$T_1 \approx \frac{Q_0(\beta_1 + \nu_1 N)}{f_1(N)} = h_{21}(N), \quad T_2 \approx \frac{\lambda N(\beta_2 + \nu_2 N)}{f_2(N)} = h_{22}(N),$$

$$U_1 \approx \frac{Q_0 \alpha_1 N}{f_1(N)} = g_{21}(N), \quad U_2 \approx \frac{\lambda \alpha_2 N^2}{f_2(N)} = g_{22}(N) \quad (4.1)$$

where $f_1(N)$, $f_2(N)$, $g_{21}(N)$, $g_{22}(N)$, $h_{21}(N)$ and $h_{22}(N)$ are same as given in (3.1d), (3.6b-f).

We note that T_i and U_i now become functions of N only and they increase as Q_0 or λ increases and hence $r(U_1(N), U_2(N))$ and $K(T_1(N), T_2(N))$ decrease with Q_0 or λ .

In this case the model (2.1) reduces to

$$\frac{dN}{dt} = \left[r(U_1(N), U_2(N)) - \frac{r_0 N}{K(T_1(N), T_2(N))} \right] N \quad (4.2)$$

with $N(0) = N_0 \geq 0$.

The above equation (4.2), is a generalized logistic equation.

Thus, the above system has only two equilibrium points $N = 0$ and $N = \tilde{N}$ where \tilde{N} is obtained by solving (3.6h) i.e.

$$F_2(N) = 0, \text{ where}$$

$$F_2(N) = r_0 N - r(g_{21}(N), g_{22}(N)) K(h_{21}(N), h_{22}(N))$$

and is same as defined by (3.6g). \tilde{N} exists uniquely as shown before in section § 3.2.

Using a comparison theorem, it can be noted from (4.2) that

$$\frac{dN}{dt} \leq r_0 \left(1 - \frac{N}{K_0} \right) N \quad (4.3)$$

This implies that $0 < \tilde{N} < K_0$.

Since U_i and T_i ($i = 1, 2$) increase as Q_0 or λ increases. Therefore \tilde{N} decreases as Q_0 or λ increases and when Q_0 or λ becomes very large then \tilde{N} may even tend to zero. This implies that the species may not survive for large emission rates.

We can check that $N = 0$ is unstable. To find the behavior of \tilde{N} , we proceed as follows:

Consider the following positive definite function about \tilde{N}

$$V_2(N) = (N - \tilde{N} - \tilde{N} \ln \frac{N}{\tilde{N}})$$

Differentiating V_2 with respect to t along the solution of the model (4.2), we get

$$\begin{aligned} \frac{dV_2}{dt} &= (N - \tilde{N}) \left[r(U_1(N), U_2(N)) - \frac{r_0 N}{K(T_1(N), T_2(N))} \right] \\ &= (N - \tilde{N}) \left[r(U_1(N), U_2(N)) - r(U_1(\tilde{N}), U_2(N)) + r(U_1(\tilde{N}), U_2(N)) \right. \\ &\quad - r(U_1(\tilde{N}), U_2(\tilde{N})) - \frac{r_0 N}{K(T_1(N), T_2(N))} + \frac{r_0 \tilde{N}}{K(T_1(\tilde{N}), T_2(N))} \\ &\quad \left. - \frac{r_0 \tilde{N}}{K(T_1(\tilde{N}), T_2(N))} + \frac{r_0 \tilde{N}}{K(T_1(\tilde{N}), T_2(\tilde{N}))} \right] \\ &= (N - \tilde{N})^2 \left[\xi_{21}(N) + \xi_{22}(N) - \frac{r_0}{K(T_1(N), T_2(N))} \right. \\ &\quad \left. - r_0 \tilde{N} \left\{ \eta_{21}(N) + \eta_{22}(N) \right\} \right] \end{aligned} \quad (4.4)$$

where

$$\xi_{21}(N) = \begin{cases} [r(U_1(N), U_2(N)) - r(U_1(\tilde{N}), U_2(N))] / (N - \tilde{N}), & N \neq \tilde{N} \\ \left. \frac{\partial r}{\partial U_1}(U_1(N), U_2(N)) \frac{dU_1}{dN} \right|_{N = \tilde{N}}, & N = \tilde{N} \end{cases}$$

$$\xi_{22}(N) = \begin{cases} [r(U_1(\tilde{N}), U_2(N)) - r(U_1(\tilde{N}), U_2(\tilde{N}))] / (N - \tilde{N}), & N \neq \tilde{N} \\ \left. \frac{\partial r}{\partial U_2}(U_1(\tilde{N}), U_2(N)) \frac{dU_2}{dN} \right|_{N = \tilde{N}}, & N = \tilde{N} \end{cases}$$

$$\begin{aligned}
\eta_{21}(N) &= \begin{cases} \frac{\frac{1}{K(T_1(N), T_2(N))} - \frac{1}{K(T_1(\tilde{N}), T_2(N))}}{N - \tilde{N}}, & N \neq \tilde{N} \\ - \frac{1}{K^2(T_1(N), T_2(N))} \frac{\partial K}{\partial T_1}(T_1(N), T_2(N)) \frac{dT_1}{dN} \Big|_{N = \tilde{N}}, & N = \tilde{N} \end{cases} \\
\eta_{22}(N) &= \begin{cases} \frac{\frac{1}{K(T_1(\tilde{N}), T_2(N))} - \frac{1}{K(T_1(\tilde{N}), T_2(\tilde{N}))}}{N - \tilde{N}}, & N \neq \tilde{N} \\ - \frac{1}{K^2(T_1(\tilde{N}), T_2(N))} \frac{\partial K}{\partial T_2}(T_1(\tilde{N}), T_2(N)) \frac{dT_2}{dN} \Big|_{N = \tilde{N}}, & N = \tilde{N} \end{cases}
\end{aligned} \tag{4.5}$$

Let $r(U_1(N), U_2(N))$ and $K(T_1(N), T_2(N))$ satisfy the following conditions

$$\begin{aligned}
K_{m1} &\leq K(T_1(N), T_2(N)) \leq K_0, \quad 0 \leq - \frac{\partial r}{\partial U_1}(U_1(N), U_2(N)) \frac{dU_1}{dN}(\tilde{N}) \leq \rho_{21}, \\
0 &\leq - \frac{\partial r}{\partial U_2}(U_1(N), U_2(N)) \frac{dU_2}{dN} \leq \rho_{22}, \quad 0 \leq - \frac{\partial K}{\partial T_1}(T_1(N), T_2(N)) \frac{dT_1}{dN}(\tilde{N}) \leq k_{21} \\
0 &\leq - \frac{\partial K}{\partial T_2}(T_1(N), T_2(N)) \frac{dT_2}{dN}(\tilde{N}) \leq k_{22}
\end{aligned} \tag{4.6}$$

for some positive constants K_{m1} , ρ_{21} , ρ_{22} , k_{21} and k_{22} .

From (4.5), (4.6) and the mean value theorem, we note that

$$\begin{aligned}
|\xi_{21}(N)| &\leq \rho_{21}, \quad |\xi_{22}(N)| \leq \rho_{22}, \quad |\eta_{21}(N)| \leq k_{21}/K_{m1}^2 \quad \text{and} \\
|\eta_{22}(N)| &\leq k_{22}/K_{m1}^2
\end{aligned} \tag{4.7}$$

Now $\frac{dV_2}{dt}$ can further be written as

$$\frac{dV_2}{dt} \leq (N - \tilde{N})^2 \left[(\rho_{21} + \rho_{22}) - \frac{r_0}{K_0} - r_0 \tilde{N} \left(\frac{k_{21} + k_{22}}{K_{m1}^2} \right) \right]$$

Thus $\frac{dV_2}{dt}$ will be negative definite provided

$$r_0 \left[\frac{1}{K_0} + \tilde{N} \left(\frac{k_{21} + k_{22}}{K_{m1}^2} \right) \right] > \rho_{21} + \rho_{22} \quad (4.8)$$

Hence V_2 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium $N = \tilde{N}$ and hence this equilibrium is globally asymptotically stable provided the condition (4.8) is satisfied.

The theorems in § 3.2 and § 3.3 show that when the inequalities (3.15) hold, the population will settle down to a much lower equilibrium level than its initial carrying capacity, the magnitude of which will depend upon the toxicity, emission and washout rate of each of the toxicants and will be much less than the case of a single toxicant having same characteristics as one of them. It is further noted that if the emission of each of the toxicants is continued without control, the population may be doomed to extinction sooner than the case of a single toxicant having the same toxicity and the emission rate as one of them, the extinction rate becoming faster with the increase in the emission rate and toxicity of the other toxicant.

4. NUMERICAL EXAMPLE

To explain the applicability of the results discussed above we consider the following particular form of $r(U_1, U_2)$ and $K(T_1, T_2)$.

$$r(U_1, U_2) = r_0 - \frac{a_1 U_1}{1 + r_1 U_1} - \frac{a_2 U_2}{1 + r_2 U_2} \quad (5.1a)$$

$$K(T_1, T_2) = K_0 - \frac{b_1 T_1}{1 + m_1 T_1} - \frac{b_2 T_2}{1 + m_2 T_2} \quad (5.1b)$$

where the coefficients are chosen as follows:

$$a_1 = 0.01, a_2 = 0.06, b_1 = 1.1, b_2 = 1.2, r_1 = 2.2, r_2 = 2.1, m_1 = 1.02, m_2 = 1.01, r_0 = 0.7, K_0 = 4.0. \quad (5.2)$$

In the model (2.1), we further choose the values of the other parameters as follows:

$$\alpha_1 = 0.002, \alpha_2 = 0.2, \beta_1 = 15.0, \beta_2 = 16.0, \delta_1 = 14.0, \delta_2 = 12.0, \\ \nu_1 = 0.03, \nu_2 = 0.02, \pi_1 = 0.05, \pi_2 = 0.06, Q_0 = 20.0, \lambda = 0.4. \quad (5.3)$$

It can be checked that all the conditions for the existence of E_4 are satisfied and E_4 is computed as follows:

$$N^* = 3.247295, T_1^* = 1.427909, T_2^* = 0.102687, U_1^* = 0.000614, U_2^* = 0.004151.$$

It can be verified that all the conditions (3.12) in Theorem 3.3 are also satisfied for the above set of parameters and hence E_4 is locally asymptotically stable.

We note from (5.1) that

$$-\frac{\partial r}{\partial U_1} = \frac{1}{(1 + r_1 U_1)^2} \leq 1, \quad -\frac{\partial r}{\partial U_2} = \frac{1}{(1 + r_2 U_2)^2} \leq 1, \\ -\frac{\partial K}{\partial T_1} = \frac{1}{(1 + m_1 T_1)^2} \leq 1, \quad -\frac{\partial K}{\partial T_2} = \frac{1}{(1 + m_2 T_2)^2} \leq 1. \quad (5.4)$$

Along with the values of the parameters chosen above, if we further choose

$$\rho_1 = \rho_2 = k_1 = k_2 = 1 \text{ and } K_m = 2.0. \quad (5.5)$$

then it can be checked that all the conditions of Theorem 3.4 are also satisfied and E_4 is globally asymptotically stable.

In table (1), the equilibrium point E_4 for different values of λ has been computed, also the conditions for its local and global stability are verified. It is found that as λ increases, N^* decreases, while there is a very slight increase in T_1^* , T_2^* also increases considerably, U_1^* decreases whereas U_2^* increases. For $\lambda = 0.4$, the second condition of global stability viz. (3.15b) is not satisfied.

λ	N^*	T_1^*	T_2^*	U_1^*	U_2^*
0.01	3.357334	1.427887	0.002650	0.000635	0.000111
0.02	3.354137	1.427887	0.005294	0.000634	0.000221
0.05	3.344692	1.427889	0.013201	0.000633	0.000550
0.1	3.329388	1.427893	0.026287	0.000630	0.001089
0.2	3.300266	1.427898	0.052137	0.000624	0.002142
0.4	3.247295	1.427909	0.102687	0.000614	0.004151
0.5	3.223087	1.427914	0.127451	0.000610	0.005114

Table (1)

5. CONCLUSION

In this Chapter, a mathematical model is proposed and analyzed to study the simultaneous effects of two different toxicants on a biological species (one toxicant being emitted in to the environment by some external source such as industries, etc. and the other is being produced by the biological species itself such as from household discharges, as in the case of human population). The cases of instantaneous spill and constant emissions of the first toxicant have been considered. The existence of non trivial equilibrium has been proved and its stability behavior is analyzed in each case. It has been found that in the case of instantaneous

spill of the toxicant, the population will settle down to a lower equilibrium level than its initial carrying capacity, the magnitude of which will depend upon the toxicity, emission and washout rate of the second toxicant (emitted by the population itself) as well as on the discharge rate coefficient λ by which it is produced. Thus, in this case eventually the equilibrium level of the biological population is affected by only the toxicant, namely the second one, produced by the species itself. In the case of constant emission of the first toxicant, it is shown that the population settles down to an equilibrium level, which is lower than its initial (toxicant independent) carrying capacity and is also lower than that in the case of instantaneous emission, the magnitude of which depends upon the toxicity, emission and washout rates of each of the toxicants and on the emission rate coefficient by which the second toxicant is being discharged in the environment by the biological population. It is noted that this equilibrium decreases as the toxicity and emission rates of the two toxicants increase and is always lower than the case of single toxicant having the same characteristics as one of them. The equilibrium also decreases with the emission rate coefficient for the second toxicant in the environment by the biological species. It has also been found that in the case of uncontrolled emissions of the two toxicants, the species may be doomed to extinction sooner than the case of a single toxicant having the same toxicity, influx and washout rates as one of the two toxicants, the extinction rate being faster as the toxicity and influx rate of the other toxicant increase.

CHAPTER - IV

EFFECTS OF PRIMARY AND SECONDARY TOXICANTS ON A BIOLOGICAL SPECIES

1. INTRODUCTION

In Chapters II and III, we have studied the effects of one or more toxicants, discharged in to the environment either by the species or from some external source, on a biological population. However, in some situations, it may happen that after being emitted in to the environment, a part of the toxicant gets converted in to a secondary toxicant which in turn together with the first (primary) toxicant affects the biological species by decreasing its growth rate and carrying capacity.

In this Chapter, we, therefore, propose and analyze a non linear model to study the effects of two toxicants, one primary and the other secondary, the primary toxicant being emitted into the environment by some external source, on a biological species. This situation, in particular, is very relevant in terrestrial environment involving plant populations affected by SO_2 and H_2SO_4 (acid rain), etc. (see Shukla and Dubey, 1996; Shukla and Agrawal, 1999 and cross references).

2. MATHEMATICAL MODEL

We consider a biological population growing logistically in a polluted environment which is simultaneously affected by primary and secondary toxicants. The primary toxicant is being emitted by an external source and a part of this toxicant is converted in to a

secondary toxicant. It is assumed that the secondary toxicant is formed by the primary (first) toxicant by a rate which is proportional to the environmental concentration of the primary toxicant. The environmental concentration of the toxicants is assumed to decrease due to some natural degradation factors. It is also assumed that the rate of uptake concentration of each of the toxicants by the species is different and is same as the depletion rate of environmental concentration of the respective toxicant which is assumed to be proportional to the density of the species as well as the concentration of the toxicant present in the environment. It is considered that the growth rate of the species decreases as the uptake concentration of each of the toxicants increases where as the carrying capacity of the species with respect to the habitat decreases with the increase in the concentrations of the two toxicants in the environment.

Keeping the above in view, the system is assumed to be governed by the following differential equations (Shukla and Dubey, 1996; Shukla and Agrawal, 1999):

$$\begin{aligned}\frac{dN}{dt} &= r(U, U_s)N - \frac{r_0 N^2}{K(T, T_s)} \\ \frac{dT}{dt} &= Q(t) - \delta_1 T - \alpha_1 TN + \pi_1 \nu_1 NU - kT \\ \frac{dT_s}{dt} &= \theta kT - \delta_2 T_s - \alpha_2 T_s N + \pi_2 \nu_2 NU_s\end{aligned}\tag{2.1}$$

$$\frac{dU}{dt} = -\beta_1 U + \alpha_1 TN - \nu_1 NU$$

$$\frac{dU_s}{dt} = -\beta_2 U_s + \alpha_2 T_s N - \nu_2 NU_s$$

$$N(0) \geq 0, T(0) \geq 0, T_s(0) \geq 0, U(0) \geq c_1 T(0), U_s(0) \geq c_2 T_s(0)$$

$$c_i > 0, 0 < \theta \leq 1, 0 \leq \pi_i \leq 1, \quad i = 1, 2$$

Here $N(t)$ is the population density of the biological species. $Q(t)$ is the emission rate of the primary toxicant into the environment with concentration $T(t)$. The positive constant k is the conversion coefficient of primary toxicant to secondary toxicant in the environment. $U(t)$ and $U_s(t)$ are the respective uptake concentrations. δ_i 's ($i = 1, 2$) are the natural washout rate coefficients of $T(t)$ and $T_s(t)$ respectively, α_i 's are the depletion rate coefficients of $T(t)$ and $T_s(t)$ respectively due to uptake by the biological population. β_i 's are the natural washout rate coefficients of $U(t)$ and $U_s(t)$ respectively. ν_i 's denote the depletion rate coefficients of $U(t)$ and $U_s(t)$ respectively due to dying out of some members of the species and fraction π_i of this reentering into the environment. c_i 's are constants relating to the initial uptake concentration $U(0)$ and $U_s(0)$ respectively with the initial environmental concentrations $T(0)$ and $T_s(0)$, θ is a fraction ≤ 1 , which represents the magnitude of the primary toxicant transformation in to secondary toxicant, as it may happen that the entire part of the primary toxicant available for transformation (i.e. " kT ") may not be transformed completely in to secondary toxicant and there may be several other compounds produced which are harmless to the biological population, not considered in the model. In an ideal situation, when $\theta = 1$, the entire primary toxicant (" kT ") gets transformed to the secondary toxicant. All the constants taken in the model, are assumed to be positive.

In writing down the model (2.1), it is also assumed that the growth rates of uptake concentrations $U(t)$ and $U_s(t)$, i.e. $\alpha_1 TN$ and

$\alpha_2 T_S N$ are same as the depletion rates of the toxicant having environmental concentration T and T_S respectively.

In the model (2.1), the function $r(U, U_S)$ represents the growth rate coefficient of biological species which decreases with the increase of U and U_S . Hence we take

$$r(0,0) = r_0 > 0, \quad \frac{\partial r}{\partial U} < 0, \quad \frac{\partial r}{\partial U_S} < 0 \quad \text{for } U > 0, U_S > 0 \quad (2.2)$$

where r_0 is the toxicant independent growth rate coefficient.

Similarly the function $K(T, T_S)$, the carrying capacity (i.e. the maximum population density which the environment can support), decreases as T and T_S increase. Hence we take

$$K(0,0) = K_0 > 0, \quad K(T, T_S) > 0 \quad \text{for } T > 0, T_S > 0$$

$$\frac{\partial K}{\partial T} < 0, \quad \frac{\partial K}{\partial T_S} < 0 \quad \text{for } T > 0, T_S > 0 \quad (2.3)$$

where K_0 is the toxicant independent carrying capacity.

3. STABILITY ANALYSIS

In the following, we analyze the model (2.1) for the case $Q(t) = Q_0$, a positive constant, only. Here we have not considered the case of instantaneous emission i.e. $Q(t) = 0$, because in such a situation the transformation from primary to secondary toxicant may be negligible as the emission takes place at $t = 0$ only.

Our model (2.1) has two nonnegative equilibria, namely $E_1(0, \frac{Q_0}{\delta_1 + k}, \frac{Q_0 \theta k}{(\delta_1 + k)\delta_2}, 0, 0)$ and $E_2(N^*, T^*, T_S^*, U^*, U_S^*)$. The existence of E_1 is obvious. We show the existence of E_2 as follows:

Here N^*, T^*, T_S^*, U^* and U_S^* are the positive solution of the system of algebraic equations given below.

$$N = r(U, U_s) K(T, T_s) / r_0 \quad (3.1a)$$

$$T = \frac{Q_0 (\beta_1 + \nu_1 N)}{f_1(N)} = h_1(N) \quad (\text{say}) \quad (3.1b)$$

$$T_s = \frac{\theta k (\beta_2 + \nu_2 N)}{f_2(N)} \frac{Q_0 (\beta_1 + \nu_1 N)}{f_1(N)} = h_2(N) \quad (\text{say}) \quad (3.1c)$$

$$U = \frac{Q_0 \alpha_1 N}{f_1(N)} = g_1(N) \quad (\text{say}) \quad (3.1d)$$

$$U_s = \frac{\theta k \alpha_2 N}{f_2(N)} \frac{Q_0 (\beta_1 + \nu_1 N)}{f_1(N)} = g_2(N) \quad (\text{say}) \quad (3.1e)$$

where

$$f_1(N) = (\delta_1 + k) \beta_1 + \left\{ \alpha_1 \beta_1 + \nu_1 (\delta_1 + k) \right\} N + (1 - \pi_1) \alpha_1 \nu_1 N^2 > 0 \quad (3.1f)$$

$$f_2(N) = \delta_2 \beta_2 + (\alpha_2 \beta_2 + \nu_2 \delta_2) N + (1 - \pi_2) \alpha_2 \nu_2 N^2 > 0 \quad (3.1g)$$

We note that T , T_s , U and U_s increase as Q_0 , θ and k increase correspondingly and thus $r(U, U_s)$ and $K(T, T_s)$ decrease with increase in these parameters.

Substituting the values of T , T_s , U , U_s in (3.1a) we get

$$r_0 N = r(g_1(N), g_2(N)) K(h_1(N), h_2(N))$$

$$\text{Let } F(N) = r_0 N - r(g_1(N), g_2(N)) K(h_1(N), h_2(N)) \quad (3.2a)$$

To show the existence of E_2 , it suffices to show that equation (3.2a) has a unique positive solution in N .

We may note that,

$$F(0) = - r(g_1(0), g_2(0)) K(h_1(0), h_2(0)) < 0 \quad \text{and}$$

$$F(K_0) = r_0 K_0 - r(g_1(K_0), g_2(K_0)) K(h_1(K_0), h_2(K_0)) > 0.$$

Thus, there exists a N^* in the interval $0 < N^* < K_0$ such that $F(N^*) = 0$.

For N^* to be unique, we must have

$$\begin{aligned} \frac{dF}{dN} = & r_0 - K(h_1(N), h_2(N)) \left[\frac{\partial r}{\partial U} \frac{dg_1}{dN} + \frac{\partial r}{\partial U_s} \frac{dg_2}{dN} \right] \\ & - r(g_1(N), g_2(N)) \left[\frac{\partial K}{\partial T} \frac{dh_1}{dN} + \frac{\partial K}{\partial T_s} \frac{dh_2}{dN} \right] > 0. \end{aligned} \quad (3.2b)$$

Since $\frac{\partial r}{\partial U}$, $\frac{\partial r}{\partial U_s}$, $\frac{\partial K}{\partial T}$ and $\frac{\partial K}{\partial T_s}$ are negative, the above condition is satisfied automatically if $\frac{dg_1}{dN}$, $\frac{dg_2}{dN}$, $\frac{dh_1}{dN}$ and $\frac{dh_2}{dN}$ are positive.

Now to study the stability behavior of E_1 and E_2 , we compute the variational matrices M_1 and M_2 corresponding to E_1 and E_2 as follows:

$$M_1 = \begin{bmatrix} r_0 & 0 & 0 & 0 & 0 \\ -\alpha_1 \hat{T} & -(\delta_1 + k) & 0 & 0 & 0 \\ -\alpha_2 \hat{T}_s & \theta k & -\delta_2 & 0 & 0 \\ \alpha_1 \hat{T} & 0 & 0 & -\beta_1 & 0 \\ \alpha_2 \hat{T}_s & 0 & 0 & 0 & -\beta_2 \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -\frac{r_0 N^*}{h(T^*, T_s^*)} & P_1 N^* & P_2 N^* & Q_1 N^* & Q_2 N^* \\ -G_1 & -(\delta_1 + k + \alpha_1 N^*) & 0 & \pi_1 \nu_1 N^* & 0 \\ -G_2 & \theta k & -(\delta_2 + \alpha_2 N^*) & 0 & \pi_2 \nu_2 N^* \\ H_1 & \alpha_1 N^* & 0 & -(\beta_1 + \nu_1 N^*) & 0 \\ H_2 & 0 & \alpha_2 N^* & 0 & -(\beta_2 + \nu_2 N^*) \end{bmatrix}$$

where

$$\begin{aligned}
\hat{T} &= \frac{Q_0}{\delta_1 + k}, \quad \hat{T}_S = \frac{Q_0 \theta k}{(\delta_1 + k) \delta_2}, \\
P_1 &= \frac{r_0 N^*}{K^2(T^*, T_S^*)} \frac{\partial K}{\partial T}(T^*, T_S^*), \quad P_2 = \frac{r_0 N^*}{K^2(T^*, T_S^*)} \frac{\partial K}{\partial T_S}(T^*, T_S^*), \\
Q_1 &= \frac{\partial r}{\partial U}(U^*, U_S^*), \quad Q_2 = \frac{\partial r}{\partial U_S}(U^*, U_S^*), \\
G_1 &= \alpha_1 T^* - \pi_1 \nu_1 U^*, \quad G_2 = \alpha_2 T_S^* - \pi_2 \nu_2 U_S^*, \\
H_1 &= \alpha_1 T^* - \nu_1 U^*, \quad H_2 = \alpha_2 T_S^* - \nu_2 U_S^* \quad (3.3)
\end{aligned}$$

From M_1 , we note that E_1 is a saddle point with stable manifold locally in the T - T_S - U - U_S space and unstable manifold locally in the N direction.

From M_2 , we can not say much about the nature of E_2 , hence we use the method of Lyapunov's function to study its behavior. Thus, we find the sufficient conditions under which E_2 is locally asymptotically stable in the form of following theorem.

THEOREM 3.1 Let the following inequalities hold

$$\left[\frac{r_0 N^*}{K^2(T^*, T_S^*)} \frac{\partial K(T^*, T_S^*)}{\partial T} - \alpha_1 T^* + \pi_1 \nu_1 U^* \right]^2 < \frac{1}{3} \frac{r_0}{K(T^*, T_S^*)} (\delta_1 + k + \alpha_1 N^*) \quad (3.4a)$$

$$\left[\frac{r_0 N^*}{K^2(T^*, T_S^*)} \frac{\partial K(T^*, T_S^*)}{\partial T_S} - \alpha_2 T_S^* + \pi_2 \nu_2 U_S^* \right]^2 < \frac{1}{3} \frac{r_0}{K(T^*, T_S^*)} (\delta_2 + \alpha_2 N^*) \quad (3.4b)$$

$$\left[\frac{\partial r(U^*, U_S^*)}{\partial U} + \alpha_1 T^* - \nu_1 U^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T^*, T_S^*)} (\beta_1 + \nu_1 N^*) \quad (3.4c)$$

$$\left[\frac{\partial r(U^*, U_S^*)}{\partial U_S} + \alpha_2 T_S^* - \nu_2 U_S^* \right]^2 < \frac{1}{2} \frac{r_0}{K(T^*, T_S^*)} (\beta_2 + \nu_2 N^*) \quad (3.4d)$$

$$(\theta k)^2 < \frac{4}{9} (\delta_1 + k + \alpha_1 N^*) (\delta_2 + \alpha_2 N^*) \quad (3.4e)$$

$$\left[\pi_1 \nu_1 + \alpha_1 \right]^2 N^{*2} < \frac{2}{3} (\delta_1 + k + \alpha_1 N^*) (\beta_1 + \nu_1 N^*) \quad (3.4f)$$

$$\left[\pi_2 \nu_2 + \alpha_2 \right]^2 N^{*2} < \frac{2}{3} (\delta_2 + \alpha_2 N^*) (\beta_2 + \nu_2 N^*) \quad (3.4g)$$

Then E_2 is locally asymptotically stable.

PROOF: Linearizing the system (2.1) about E_2 and assuming

$$N = N^* + n, \quad T = T^* + \tau, \quad T_s = T_s^* + \tau_s, \quad U = U^* + u$$

and $U_s = U_s^* + u_s$ where n, τ, τ_s, u and u_s are small perturbations around E_2 . We get the following linearized system of (2.1)

$$\dot{n} = N^* \left[- \frac{r_0}{K(T^*, T_s^*)} n + P_1 \tau + P_2 \tau_s + Q_1 u + Q_2 u_s \right]$$

$$\dot{\tau} = -G_1 n - (\delta_1 + k + \alpha_1 N^*) \tau + \pi_1 \nu_1 N^* u$$

$$\dot{\tau}_s = -G_2 n + \theta k \tau - (\delta_2 + \alpha_2 N^*) \tau_s + \pi_2 \nu_2 N^* u_s$$

$$\dot{u} = H_1 n + \alpha_1 N^* \tau - (\beta_1 + \nu_1 N^*) u$$

$$\dot{u}_s = H_2 n + \alpha_2 N^* \tau_s - (\beta_2 + \nu_2 N^*) u_s \quad (3.5)$$

Now consider the following positive definite function

$$V = \frac{1}{2} n^2 + \frac{1}{2} \tau^2 + \frac{1}{2} \tau_s^2 + \frac{1}{2} u^2 + \frac{1}{2} u_s^2 \quad (3.6)$$

Then $\dot{V} = n\dot{n} + \tau\dot{\tau} + \tau_s\dot{\tau}_s + u\dot{u} + u_s\dot{u}_s$

Substituting values of \dot{n} , $\dot{\tau}$, $\dot{\tau}_s$, \dot{u} and \dot{u}_s from (3.5) in to equation (3.6) and doing same algebraic manipulation, we get

$$\begin{aligned}\dot{V} = & -\frac{1}{2} a_{11} n^2 + a_{12} n\tau - \frac{1}{2} a_{22} \tau^2 \\ & -\frac{1}{2} a_{11} n^2 + a_{13} n\tau_s - \frac{1}{2} a_{33} \tau_s^2 \\ & -\frac{1}{2} a_{11} n^2 + a_{14} nu - \frac{1}{2} a_{44} u^2 \\ & -\frac{1}{2} a_{11} n^2 + a_{15} nu_s - \frac{1}{2} a_{55} u_s^2 \\ & -\frac{1}{2} a_{22} \tau^2 + a_{23} \tau\tau_s - \frac{1}{2} a_{33} \tau_s^2 \\ & -\frac{1}{2} a_{22} \tau^2 + a_{24} \tau u - \frac{1}{2} a_{44} u^2 \\ & -\frac{1}{2} a_{33} \tau_s^2 + a_{35} \tau_s u_s - \frac{1}{2} a_{55} u_s^2\end{aligned}\quad (3.7)$$

$$\text{where } a_{11} = \frac{1}{2} \frac{r_0}{K(T^*, T_s^*)}, \quad a_{22} = \frac{2}{3} (\delta_1 + k + \alpha_1 N^*),$$

$$a_{33} = \frac{2}{3} (\delta_2 + \alpha_2 N^*), \quad a_{44} = (\beta_1 + \nu_1 N^*), \quad a_{55} = (\beta_2 + \nu_2 N^*),$$

$$a_{12} = P_1 - G_1 = \frac{r_0 N^*}{K^2(T^*, T_s^*)} \frac{\partial K(T^*, T_s^*)}{\partial T} - \alpha_1 T^* + \pi_1 \nu_1 U^*,$$

$$a_{13} = P_2 - G_2 = \frac{r_0 N^*}{K^2(T^*, T_s^*)} \frac{\partial K(T^*, T_s^*)}{\partial T_s} - \alpha_2 T_s^* + \pi_2 \nu_2 U_s^*,$$

$$a_{14} = Q_1 + H_1 = \frac{\partial r(U^*, U_s^*)}{\partial U} + \alpha_1 T^* - \nu_1 U^*,$$

$$a_{15} = Q_2 + H_2 = \frac{\partial r(U^*, U_s^*)}{\partial U} + \alpha_2 T_s^* - \nu_2 U_s^*,$$

$$a_{23} = \theta k, \quad a_{24} = (\pi_1 \nu_1 + \alpha_1) N^* \quad \text{and} \quad a_{35} = (\pi_2 \nu_2 + \alpha_2) N^* \quad (3.8)$$

From (3.7) and (3.8) we note that \dot{V} is negative definite provided

$$\begin{aligned} a_{12}^2 < a_{11}a_{22}, \quad a_{13}^2 < a_{11}a_{33}, \quad a_{14}^2 < a_{11}a_{44}, \quad a_{15}^2 < a_{11}a_{55}, \\ a_{23}^2 < a_{22}a_{33}, \quad a_{24}^2 < a_{22}a_{44}, \quad a_{35}^2 < a_{33}a_{55} \end{aligned} \quad (3.9)$$

The conditions (3.9), in view of (3.8) respectively give the conditions (3.4).

This shows that under the conditions (3.9), \dot{V} is negative definite showing that V is a Lyapunov's function for the linearized system and hence the proof of the theorem (3.1) follows.

Now to show that E_2 is globally asymptotically stable, we first need a lemma which establishes the region of attraction for the system (2.1).

LEMMA 3.1 The set

$$\Omega = \left\{ (N, T, T_s, U, U_s) : 0 \leq N \leq K_0, \quad 0 \leq T + U \leq \frac{Q_0}{\delta_{m1}}, \right. \\ \left. 0 \leq T_s + U_s \leq \frac{\theta k Q_0}{\delta_{m1} \delta_{m2}} \right\}$$

where $\delta_{m1} = \min(\delta_1 + k, \beta_1)$ and $\delta_{m2} = \min(\delta_2, \beta_2)$

is a region of attraction for all solutions initiating in the positive orthant.

PROOF: From (2.1) we have

$$\begin{aligned} \frac{dN}{dt} &= r(U, U_s)N - \frac{r_0 N^2}{K(T, T_s)} \\ &\leq r_0 N - \frac{r_0 N^2}{K_0} \end{aligned}$$

hence $\limsup_{t \rightarrow \infty} N(t) = K_0$

We also have

$$\begin{aligned}\frac{dT}{dt} + \frac{dU}{dt} &= Q_0 - \delta_1 T_1 - \beta_1 U_1 - kT - (1 - \pi_1) \nu_1 N U_1 \\ &\leq Q_0 - \delta_{m1} (T + U) \quad \text{where } \delta_{m1} = \min (\delta_1 + k, \beta_1)\end{aligned}$$

This implies that

$$\limsup_{t \rightarrow \infty} [T(t) + U(t)] = \frac{Q_0}{\delta_{m1}}$$

similarly

$$\begin{aligned}\frac{dT_s}{dt} + \frac{dU_s}{dt} &= \theta k T - \delta_2 T_s - \beta_2 U_s - (1 - \pi_2) \nu_2 N U_s \\ &\leq \theta k \frac{Q_0}{\delta_{m1}} - \delta_{m2} (T_s + U_s) \quad \text{where } \delta_{m2} = \min (\delta_2, \beta_2)\end{aligned}$$

$$\limsup_{t \rightarrow \infty} [T_s(t) + U_s(t)] = \frac{\theta k Q_0}{\delta_{m1} \delta_{m2}}$$

and hence the proof of the lemma.

THEOREM 3.2 In addition to the assumptions (2.2) and (2.3), let $r(U, U_s)$ and $K(T, T_s)$ satisfy the following conditions in Ω ,

$$K_m \leq K(T, T_s) \leq K_0, \quad 0 \leq -\frac{\partial r}{\partial U}(U, U_s) \leq \rho_1, \quad 0 \leq -\frac{\partial r}{\partial U_s}(U, U_s) \leq \rho_2$$

$$0 \leq -\frac{\partial K}{\partial T}(T, T_s) \leq k_1, \quad 0 \leq -\frac{\partial K}{\partial T_s}(T, T_s) \leq k_2 \quad (3.10)$$

for some positive constants $K_m, \rho_1, \rho_2, k_1, k_2$.

Then if the following inequalities hold

$$\left[\frac{r_0 k_1 K_0}{K_m^2} + (\alpha_1 + \pi_1 \nu_1) \frac{Q_0}{\delta_{m1}} \right]^2 < \frac{1}{3} \frac{r_0}{K(T^*, T_s^*)} (\delta_1 + k + \alpha_1 N^*) \quad (3.11a)$$

$$\left[\frac{r_0 k_2 K_0}{K_m^2} + (\alpha_2 + \pi_2 \nu_2) \frac{\theta k Q_0}{\delta_{m1} \delta_{m2}} \right]^2 < \frac{1}{3} \frac{r_0}{K(T^*, T_s^*)} (\delta_2 + \alpha_2 N^*) \quad (3.11b)$$

$$\left[\rho_1 + (\alpha_1 + \nu_1) \frac{Q_0}{\delta_{m1}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T^*, T_s^*)} (\beta_1 + \nu_1 N^*) \quad (3.11c)$$

$$\left[\rho_2 + (\alpha_2 + \nu_2) \frac{\theta k Q_0}{\delta_{m1} \delta_{m2}} \right]^2 < \frac{1}{2} \frac{r_0}{K(T^*, T_S^*)} (\beta_2 + \nu_2 N^*) \quad (3.11d)$$

$$(\theta k)^2 < \frac{4}{9} (\delta_1 + k + \alpha_1 N^*) (\delta_2 + \alpha_2 N^*) \quad (3.11e)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N^* \right]^2 < \frac{2}{3} (\delta_1 + k + \alpha_1 N^*) (\beta_1 + \nu_1 N^*) \quad (3.11f)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N^* \right]^2 < \frac{2}{3} (\delta_2 + \alpha_2 N^*) (\beta_2 + \nu_2 N^*) \quad (3.11g)$$

E_2 is globally asymptotically stable in Ω .

PROOF:

We consider the following positive definite function about E_2 ,

$$\begin{aligned} V_1(N, T, T_S, U, U_S) = & (N - N^* - N^* \ln \frac{N}{N^*}) + \frac{1}{2} (T - T^*)^2 \\ & + \frac{1}{2} (T_S - T_S^*)^2 + \frac{1}{2} (U - U^*)^2 + \frac{1}{2} (U_S - U_S^*)^2 \end{aligned}$$

Differentiating V_1 with respect to t along the solution of the model (2.1), we get

$$\begin{aligned} \frac{dV_1}{dt} = & (N - N^*) \left[r(U, U_S) - \frac{r_0 N}{K(T, T_S)} \right] \\ & + (T - T^*) \left[Q_0 - \delta_1 T - \alpha_1 T N - kT + \pi_1 \nu_1 N U \right] \\ & + (T_S - T_S^*) \left[\theta k T - \delta_2 T_S - \alpha_2 T_S N + \pi_2 \nu_2 N U_S \right] \\ & + (U - U^*) \left[-\beta_1 U + \alpha_1 T N - \nu_1 N U \right] \\ & + (U_S - U_S^*) \left[-\beta_2 U_S + \alpha_2 T_S N - \nu_2 N U_S \right] \end{aligned} \quad (3.12)$$

Using (3.1) and simplifying, we get

$$\begin{aligned}
\frac{dV_1}{dt} = & - \frac{r_0}{K(T^*, T_S^*)} (N - N^*)^2 - (\delta_1 + k + \alpha_1 N^*) (T - T^*)^2 \\
& - (\delta_2 + \alpha_2 N^*) (T_S - T_S^*)^2 - (\beta_1 + \nu_1 N^*) (U - U^*)^2 \\
& - (\beta_2 + \nu_2 N^*) (U_S - U_S^*)^2 \\
& - (N - N^*) (T - T^*) [r_0 N \eta_1(T, T_S) + \alpha_1 T - \pi_1 \nu_1 U] \\
& - (N - N^*) (T_S - T_S^*) [r_0 N \eta_2(T^*, T_S) + \alpha_2 T_S - \pi_2 \nu_2 U_S] \\
& + (N - N^*) (U - U^*) [\xi_1(U, U_S) + \alpha_1 T - \nu_1 U] \\
& + (N - N^*) (U_S - U_S^*) [\xi_2(U^*, U_S) + \alpha_2 T_S - \nu_2 U_S] \\
& + (T - T^*) (T_S - T_S^*) [\theta k] \\
& + (T - T^*) (U - U^*) [\pi_1 \nu_1 N^* + \alpha_1 N^*] \\
& + (T_S - T_S^*) (U_S - U_S^*) [\pi_2 \nu_2 N^* + \alpha_2 N^*]
\end{aligned} \tag{3.13}$$

where

$$\xi_1(U, U_S) = \begin{cases} [r(U, U_S) - r(U^*, U_S)] / (U - U^*), & U \neq U^* \\ \frac{\partial r}{\partial U}(U, U_S), & U = U^* \end{cases} \tag{3.14a}$$

$$\xi_2(U^*, U_S) = \begin{cases} [r(U^*, U_S) - r(U^*, U_S^*)] / (U_S - U_S^*), & U_S \neq U_S^* \\ \frac{\partial r}{\partial U_S}(U^*, U_S), & U_S = U_S^* \end{cases} \tag{3.14b}$$

$$\eta_1(T, T_S) = \begin{cases} [\frac{1}{K(T, T_S)} - \frac{1}{K(T^*, T_S)}] / (T - T^*), & T \neq T^* \\ - \frac{1}{K^2(T^*, T_S)} \frac{\partial K}{\partial T}(T^*, T_S), & T = T^* \end{cases} \tag{3.14c}$$

$$\eta_2(T^*, T_S) = \begin{cases} \left[\frac{1}{K(T^*, T_S)} - \frac{1}{K(T^*, T_S^*)} \right] / (T_S - T_S^*), & T_S \neq T_S^* \\ - \frac{1}{K^2(T^*, T_S^*)} \frac{\partial K}{\partial T_S}(T^*, T_S^*), & T_S = T_S^* \end{cases} \quad (3.14d)$$

From (3.10), (3.14) and the mean value theorem, we note that

$$|\xi_1(U, U_S)| \leq \rho_1, \quad |\xi_2(U^*, U_S)| \leq \rho_2, \quad |\eta_1(T, T_S)| \leq k_1/K_m^2 \quad \text{and} \\ |\eta_2(T^*, T_S)| \leq k_2/K_m^2 \quad (3.15)$$

Now $\frac{dV_1}{dt}$ can further be written as sum of the quadratics

$$\begin{aligned} \frac{dV_1}{dt} = & -\frac{1}{2} a_{11} (N - N^*)^2 + a_{12} (N - N^*) (T - T^*) - \frac{1}{2} a_{22} (T - T^*)^2 \\ & - \frac{1}{2} a_{11} (N - N^*)^2 + a_{13} (N - N^*) (T_S - T_S^*) - \frac{1}{2} a_{33} (T_S - T_S^*)^2 \\ & - \frac{1}{2} a_{11} (N - N^*)^2 + a_{14} (N - N^*) (U - U^*) - \frac{1}{2} a_{44} (U - U^*)^2 \\ & - \frac{1}{2} a_{11} (N - N^*)^2 + a_{15} (N - N^*) (U_S - U_S^*) - \frac{1}{2} a_{55} (U_S - U_S^*)^2 \\ & - \frac{1}{2} a_{22} (T - T^*)^2 + a_{23} (T - T^*) (T_S - T_S^*) - \frac{1}{2} a_{33} (T_S - T_S^*)^2 \\ & - \frac{1}{2} a_{22} (T - T^*)^2 + a_{24} (T - T^*) (U - U^*) - \frac{1}{2} a_{44} (U - U^*)^2 \\ & - \frac{1}{2} a_{33} (T_S - T_S^*)^2 + a_{35} (T_S - T_S^*) (U_S - U_S^*) - \frac{1}{2} a_{55} (U_S - U_S^*)^2 \end{aligned} \quad (3.16)$$

where

$$\begin{aligned} a_{11} &= \frac{1}{2} \frac{r_0}{K(T_1^*, T_2^*)}, \quad a_{22} = \frac{2}{3} (\delta_1 + k + \alpha_1 N^*), \\ a_{33} &= \frac{2}{3} (\delta_2 + \alpha_2 N^*), \quad a_{44} = \beta_1 + \nu_1 N^*, \quad a_{55} = \beta_2 + \nu_2 N^*, \\ a_{12} &= - \left[r_0 N \eta_1(T, T_S) + \alpha_1 T - \pi_1 \nu_1 U \right], \\ a_{13} &= - \left[r_0 N \eta_2(T^*, T_S) + \alpha_2 T_S - \pi_2 \nu_2 U_S \right], \end{aligned}$$

$$\begin{aligned}
a_{14} &= \xi_1(U, U_s) + \alpha_1 T - \nu_1 U, \\
a_{15} &= \xi_2(U^*, U_s) + \alpha_2 T_s - \nu_2 U_s, \\
a_{23} &= \theta k, \quad a_{24} = \pi_1 \nu_1 N^* + \alpha_1 N^*, \quad a_{35} = \pi_2 \nu_2 N^* + \alpha_2 N^* \quad (3.17)
\end{aligned}$$

The sufficient conditions for $\frac{dV_1}{dt}$ to be negative definite are that the following inequalities hold:

$$a_{12}^2 < a_{11}a_{22} \quad (3.18a)$$

$$a_{13}^2 < a_{11}a_{33} \quad (3.18b)$$

$$a_{14}^2 < a_{11}a_{44} \quad (3.18c)$$

$$a_{15}^2 < a_{11}a_{55} \quad (3.18d)$$

$$a_{23}^2 < a_{22}a_{33} \quad (3.18e)$$

$$a_{24}^2 < a_{22}a_{44} \quad (3.18f)$$

$$a_{35}^2 < a_{33}a_{55} \quad (3.18g)$$

We note that $(3.18a, b, c, d, e, f, g) \implies (3.11a, b, c, d, e, f, g)$ respectively. Hence V_1 is a Lyapunov function (La Salle and Lefschetz, 1961) with respect to E_2 whose domain contains the region of attraction Ω , proving the theorem.

4. A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANTS

We assume, in this case, that the dynamics of both the toxicant concentrations (environmental as well as uptake) for both of the toxicants, primary and secondary, are very so that their equilibria are attained with the density of the biological species almost instantaneously. In such a case, we assume :

$$\frac{dT}{dt} \approx 0, \quad \frac{dT_s}{dt} \approx 0, \quad \frac{dU}{dt} \approx 0 \text{ and } \frac{dU_s}{dt} \approx 0 \quad \text{for all } t \geq 0.$$

From last four equations of (2.1), we then have

$$T \approx \frac{Q_0(\beta_1 + \nu_1 N)}{f_1(N)} = h_1(N), \quad T_s \approx \frac{\theta k(\beta_2 + \nu_2 N)}{f_2(N)} \frac{Q_0(\beta_1 + \nu_1 N)}{f_1(N)} = h_2(N),$$

$$U \approx \frac{Q_0 \alpha_1 N}{f_1(N)} = g_1(N) \quad \text{and} \quad U_s \approx \frac{\theta k \alpha_2 N}{f_2(N)} \frac{Q_0(\beta_1 + \nu_1 N)}{f_1(N)} = g_2(N) \quad (4.1)$$

where $f_1(N)$, $f_2(N)$, $g_1(N)$, $g_2(N)$, $h_1(N)$ and $h_2(N)$ are same as given in (3.1b-f).

We note that T , T_s , U and U_s have become now functions of N only and they increase as Q_0 or k increases and hence $r(U(N), U_s(N))$ and $K(T(N), T_s(N))$ decrease with Q_0 or k .

In this case the model (2.1) reduces to

$$\frac{dN}{dt} = \left[r(U(N), U_s(N)) - \frac{r_0 N}{K(T(N), T_s(N))} \right] N \quad (4.2)$$

with $N(0) = N_0 \geq 0$.

The above equation (4.2), is a generalized logistic equation.

Thus, the above system has only two equilibrium points $N = 0$ and $N = \tilde{N}$ where \tilde{N} is obtained by solving (3.2a) i.e.

$F(N) = 0$, where

$$F(N) = r_0 N - r(g_1(N), g_2(N)) K(h_1(N), h_2(N))$$

and is the same as defined by (3.2a). \tilde{N} exists uniquely as shown before in section § 3.

Using a comparison theorem, it can be noted from (4.2) that

$$\frac{dN}{dt} \leq r_0 \left(1 - \frac{N}{K_0} \right) N \quad (4.3)$$

This implies that $0 < \tilde{N} < K_0$.

Since T , T_s , U and U_s increase as Q_0 or k increases, therefore, \tilde{N} decreases as Q_0 or k increases and further if Q_0 or k becomes very

large, then \tilde{N} may even tend to zero. This implies that the species may not survive for large emission rates.

We can check that $N = 0$ is unstable. To find the behavior of \tilde{N} , we proceed as follows:

Consider the following positive definite function about \tilde{N}

$$V_2(N) = (N - \tilde{N} - \tilde{N} \ln \frac{N}{\tilde{N}})$$

Differentiating V_2 with respect to t along the solution of the model (4.2), we get

$$\begin{aligned} \frac{dV_2}{dt} &= (N - \tilde{N}) \left[r(U(N), U_S(N)) - \frac{r_0 N}{K(T(N), T_S(N))} \right] \\ &= (N - \tilde{N}) \left[r(U(N), U_S(N)) - r(U(\tilde{N}), U_S(N)) + r(U(\tilde{N}), U_S(N)) \right. \\ &\quad - r(U(\tilde{N}), U_S(\tilde{N})) - \frac{r_0 N}{K(T(\tilde{N}), T_S(N))} + \frac{r_0 \tilde{N}}{K(T(\tilde{N}), T_S(N))} \\ &\quad \left. - \frac{r_0 \tilde{N}}{K(T(\tilde{N}), T_S(N))} + \frac{r_0 \tilde{N}}{K(T(\tilde{N}), T_S(\tilde{N}))} \right] \\ &= (N - \tilde{N})^2 \left[\xi_{21}(N) + \xi_{22}(N) - \frac{r_0}{K(T(N), T_S(N))} \right. \\ &\quad \left. - r_0 \tilde{N} \left\{ \eta_{21}(N) + \eta_{22}(N) \right\} \right] \end{aligned} \quad (4.4)$$

where

$$\xi_{21}(N) = \begin{cases} [r(U(N), U_S(N)) - r(U(\tilde{N}), U_S(N))] / (N - \tilde{N}), & N \neq \tilde{N} \\ \frac{\partial r}{\partial U}(U(N), U_S(N)) \frac{dU}{dN} \Big|_{N = \tilde{N}}, & N = \tilde{N} \end{cases}$$

$$\begin{aligned}
\xi_{22}^{(N)} &= \begin{cases} [r(U(\tilde{N}), U_S(N)) - r(U(\tilde{N}), U_S(\tilde{N}))] / (N - \tilde{N}), & N \neq \tilde{N} \\ \left. \frac{\partial r}{\partial U_S}(U(\tilde{N}), U_S(N)) \frac{dU_S}{dN} \right|_{N = \tilde{N}}, & N = \tilde{N} \end{cases} \\
\eta_{21}^{(N)} &= \begin{cases} \frac{\frac{1}{K(T(\tilde{N}), T_S(N))} - \frac{1}{K(T(\tilde{N}), T_S(N))}}{N - \tilde{N}}, & N \neq \tilde{N} \\ - \frac{1}{K^2(T(N), T_S(N))} \frac{\partial K}{\partial T}(T(N), T_S(N)) \frac{dT}{dN} \Big|_{N = \tilde{N}}, & N = \tilde{N} \end{cases} \\
\eta_{22}^{(N)} &= \begin{cases} \frac{\frac{1}{K(T(\tilde{N}), T_S(N))} - \frac{1}{K(T(\tilde{N}), T_S(\tilde{N}))}}{N - \tilde{N}}, & N \neq \tilde{N} \\ - \frac{1}{K^2(T(\tilde{N}), T_S(N))} \frac{\partial K}{\partial T_S}(T(\tilde{N}), T_S(N)) \frac{dT_S}{dN} \Big|_{N = \tilde{N}}, & N = \tilde{N} \end{cases}
\end{aligned} \tag{4.5}$$

Let $r(U(N), U_S(N))$ and $K(T(N), T_S(N))$ satisfy the following conditions

$$\begin{aligned}
K_{m1} &\leq K(T(N), T_S(N)) \leq K_0, \quad 0 \leq - \frac{\partial r}{\partial U}(U(N), U_S(N)) \frac{dU}{dN}(\tilde{N}) \leq \rho_{21}, \\
0 &\leq - \frac{\partial r}{\partial U_S}(U(N), U_S(N)) \frac{dU_S}{dN} \leq \rho_{22}, \quad 0 \leq - \frac{\partial K}{\partial T}(T(N), T_S(N)) \frac{dT}{dN}(\tilde{N}) \leq k_{21} \\
0 &\leq - \frac{\partial K}{\partial T_S}(T(N), T_S(N)) \frac{dT_S}{dN}(\tilde{N}) \leq k_{22}
\end{aligned} \tag{4.6}$$

for some positive constants K_{m1} , ρ_{21} , ρ_{22} , k_{21} and k_{22} .

From (4.5), (4.6) and the mean value theorem, we note that

$$\begin{aligned}
|\xi_{21}^{(N)}| &\leq \rho_{21}, \quad |\xi_{22}^{(N)}| \leq \rho_{22}, \quad |\eta_{21}^{(N)}| \leq k_{21}/K_{m1}^2 \quad \text{and} \\
|\eta_{22}^{(N)}| &\leq k_{22}/K_{m1}^2
\end{aligned} \tag{4.7}$$

Now $\frac{dv_2}{dt}$ can further be written as

$$\frac{dv_2}{dt} \leq (N - \tilde{N})^2 \left[(\rho_{21} + \rho_{22}) - \frac{r_0}{K_0} - r_0 \tilde{N} \left(\frac{k_{21} + k_{22}}{K_{m1}^2} \right) \right]$$

Thus $\frac{dv_2}{dt}$ will be negative definite provided

$$r_0 \left[\frac{1}{K_0} + \tilde{N} \left(\frac{k_{21} + k_{22}}{K_{m1}^2} \right) \right] > \rho_{21} + \rho_{22} \quad (4.8)$$

Hence V_2 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium $N = \tilde{N}$ and hence this equilibrium is globally asymptotically stable provided the condition (4.8) is satisfied.

The above theorems imply that when the inequalities (3.11) or (4.8) hold, the population will settle down to a lower equilibrium level than its initial carrying capacity, the magnitude of which will depend upon the toxicity, emission and washout rate of the primary toxicant and also on the rate of transformation of the secondary toxicant and it will be much less than the case of a single toxicant having same characteristics. It is further noted that if the emission of the primary toxicant is continued without control, the population may be doomed to extinction in this case also as in the previous Chapters.

4. NUMERICAL EXAMPLE

To explain the applicability of the results discussed above we consider the following particular form of $r(U, U_s)$ and $K(T, T_s)$.

$$r(U, U_s) = r_0 - \frac{a_1 U}{1 + r_1 U} - \frac{a_2 U_s}{1 + r_2 U_s} \quad (5.1a)$$

$$K(T, T_s) = K_0 - \frac{b_1 T}{1 + m_1 T} - \frac{b_2 T_s}{1 + m_2 T_s} \quad (5.1b)$$

here the coefficients are chosen as follows:

$$a_1 = 0.01, a_2 = 0.06, b_1 = 1.1, b_2 = 1.2, r_1 = 2.2, r_2 = 2.1, m_1 = 0.02, m_2 = 1.01, r_0 = 0.7, K_0 = 4.0. \quad (5.2)$$

In the model (2.1), we further choose the values of the other parameters as follows:

$$\alpha_1 = 0.002, \alpha_2 = 0.2, \beta_1 = 15.0, \beta_2 = 16.0, \delta_1 = 14.0, \delta_2 = 12.0, \nu_1 = 0.03, \nu_2 = 0.02, \pi_1 = 0.05, \pi_2 = 0.06, Q_0 = 20.0, k = 5.0, \theta = 0.5 \quad (5.3)$$

It can be checked that all the conditions for the existence of E_2 are satisfied and it can be found as follows:

$$N^* = 3.233135, T^* = 1.052274, T_s^* = 0.208017, U^* = 0.000451, U_s^* = 0.008373.$$

It can be verified that all the conditions (3.4) in Theorem 3.1 are also satisfied for the above set of parameters and hence E_2 is locally asymptotically stable.

We note from (5.1) that

$$\begin{aligned} -\frac{\partial r}{\partial U} &= \frac{1}{(1 + r_1 U)^2} \leq 1, & -\frac{\partial r}{\partial U_s} &= \frac{1}{(1 + r_2 U_s)^2} \leq 1, \\ -\frac{\partial K}{\partial T} &= \frac{1}{(1 + m_1 T)^2} \leq 1, & -\frac{\partial K}{\partial T_s} &= \frac{1}{(1 + m_2 T_s)^2} \leq 1. \end{aligned} \quad (5.4)$$

we further choose

$$\rho_1 = \rho_2 = k_1 = k_2 = 1 \text{ and } K_m = 2.0 \quad (5.5)$$

It can be checked that all the conditions of Theorem 3.2 are satisfied and E_2 is globally asymptotically stable.

Further, in table (1), we have computed E_2 for $k = 2.5$ and for two different values of θ , viz. $\theta = 0.0, 1.0$. It is found that for $\theta = 0.0$, as expected, T_s^* and U_s^* are zero and N^* is decreased for $\theta = 1.0$ whereas T^* is increased very slightly.

θ	N^*	T^*	T_s^*	U^*	U_s^*
0.0	3.403881	1.211622	0.000000	0.000546	0.000000
1.0	3.169727	1.211656	0.239765	0.000509	0.009462

Table (1)

In table (2), we have computed E_2 for $\theta = 0.5$ and different values of k and also all the conditions for its local and global stability are also verified. It is found that as k increases N^* decrease, but for large values of k , ($k = 20.0$), N^* starts decreasing and for $k = 25.0$ it is found that the second condition for the global stability i.e. (3.11b) is not satisfied. T^* and U^* decrease with increasing k , while T_s^* and U_s^* increase with k .

k	N^*	T^*	T_s^*	U^*	U_s^*
0.1	3.355671	1.417765	0.005595	0.000630	0.000234
0.5	3.337620	1.378676	0.027209	0.000609	0.001130
1.0	3.318043	1.332744	0.052622	0.000586	0.002173
5.0	3.233135	1.052274	0.208017	0.000451	0.008373
10.0	3.204350	0.833111	0.329535	0.000354	0.013147
15.0	3.202976	0.689503	0.409105	0.000293	0.016314
20.0	3.210888	0.588124	0.465214	0.000250	0.018597
25.0	3.221966	0.512736	0.506887	0.000219	0.020333

Table (2)

6. CONCLUSION

In this Chapter, we have proposed and analyzed a mathematical model to study the simultaneous effects of primary and secondary toxicants on a biological species. The primary toxicant is being emitted in to the environment with a constant prescribed rate by an external source and a part of which gets transformed in to a secondary toxicant. The existence of non trivial equilibrium has been proved and its stability behavior is studied. It has been shown that the population settles down to an equilibrium level, which is lower than its initial (toxicant independent) carrying capacity, the magnitude of which depends upon the toxicity, emission and washout rates of primary as well as secondary toxicants. It is noted that this equilibrium decreases as the toxicity and emission rate of these toxicants increase. It is further noted that the biological species is doomed to extinction if the emission rate of the primary toxicant is very large and the secondary toxicant is equally harmful.

CHAPTER - V

EFFECTS OF N - TOXICANTS EMITTED FROM EXTERNAL SOURCES ON A BIOLOGICAL POPULATION

1. INTRODUCTION

It is well known in ecological studies that ecosystems are affected by accidental spills or constant or periodic emissions of toxicants into the environment (Nelson, 1970; Hass, 1981; Jenson and Marshall, 1982; Patin, 1982). Generally the effects of toxicants are to decrease the growth rate of species and the carrying capacity of the environment. In recent decades the effect of a single toxicant on various ecosystems have been studied using mathematical models (Hallam and Clark, 1982; Hallam et al, 1983a,b; Hallam and De Luna, 1984; De Luna and Hallam, 1987; Freedman and Shukla, 1991). In particular, Hallam et al (1983) studied the effect of a toxicant emitted into the environment on a biological population by assuming that the growth rate of population density depends linearly upon the uptake concentration of this toxicant. But the effect of the environmental toxicant on the carrying capacity of the environment was not considered. However, Freedman and Shukla (1991) studied the role of a toxicant on a single species and predator - prey system by considering its effect on both the growth rate of the population as well as on the carrying capacity of the environment. Further, Shukla and Dubey (1996) proposed a model to study the simultaneous effects of two toxicants, one being more toxic than the other, on a biological

population.

It may be noted here that in the above investigations, the simultaneous effect of a number of toxicants (pollutants) emitted into the environment from different sources on a single or more biological species have not been studied though such phenomena exists both in aquatic as well as terrestrial environments (Todd and Garber, 1958; Saunders, 1975; Reinert and Gray, 1981; Patin, 1982; Cairns, 1985; Rai and Raizada, 1989; Cairns, 1990).

In this Chapter, therefore, we propose and analyze a non linear mathematical model to study the simultaneous effects of a number of toxicants (say n) on a biological population in the environment. It is assumed that all the toxicants are being emitted into the environment by different external sources. The cases of instantaneous spill and constant influx of the toxicants are considered in the model study.

2. MATHEMATICAL MODEL

We consider a single biological species affected by n non-interacting toxicants. It is assumed that each of the toxicants is emitted into the environment with an instantaneous or a constant influx and is depleted by some natural degradation factors. It is assumed further that the growth rate of the uptake concentration of each of the toxicant by this species is different and is equal to the depletion rate of the respective toxicant in the environment which is considered to be proportional to the density of the population as well as the concentrations of the toxicants in the environment. It is also assumed that the growth rate of the species

density decreases as the uptake concentrations of toxicants increase but its carrying capacity decreases with the increase of concentrations of the toxicants in the environment. Using similar arguments as Freedman and Shukla (1991), the system is assumed to be governed by the following differential equations

$$\begin{aligned}\frac{dN}{dt} &= r(U_1, \dots, U_n)N - \frac{r_0 N^2}{K(T_1, \dots, T_n)} \\ \frac{dT_i}{dt} &= Q_i(t) - \delta_i T_i - \alpha_i T_i N + \pi_i \nu_i N U_i \\ \frac{dU_i}{dt} &= -\beta_i U_i + \alpha_i T_i N - \nu_i N U_i \\ i &= 1, 2, \dots, n\end{aligned}\tag{2.1}$$

$$N(0) = N_0 \geq 0, T_i(0) = T_{i0} \geq 0, U_i(0) \geq c_i N_0, 0 \leq \pi_i \leq 1$$

Here $N(t)$ is the density of a biological species, $T_i(t)$ is the concentration of i -th toxicant emitted into the environment and $U_i(t)$ is the uptake concentration of the i -th toxicant by the species under consideration. $Q_i(t)$ is the emission rate of the i -th toxicant into the environment which is either zero or a constant. $\delta_i > 0$ is the natural washout rate coefficient of $T_i(t)$, α_i is the depletion rate coefficient of $T_i(t)$ due to its uptake by the population, β_i is the natural washout rate coefficient of $U_i(t)$, ν_i is the depletion rate coefficient of $U_i(t)$ due to dying out of some members of the species population and a fraction π_i of which reentering the environment. $c_i \geq 0$ is a constant relating to the initial uptake concentration $U_i(0)$ with the initial population N_0 . In writing down the model (2.1) it has been assumed that the growth rate of uptake concentration $U_i(t)$ is proportional to $\alpha_i T_i N$ which

is also the rate of depletion of the i -th toxicant $T_i(t)$ in the environment.

In the model (2.1), the function $r(U_1, \dots, U_n)$ represents the growth rate coefficient of the biological population which decreases with U_i . Hence we assume

$$r(0, \dots, 0) = r_0 > 0, \quad \frac{\partial r}{\partial U_i} < 0 \quad \text{for } U_i > 0, \quad i = 1, 2, \dots, n. \quad (2.2)$$

The function $K(T_1, \dots, T_n)$ in (2.1), the carrying capacity, represents the maximum population density which the environment can support and it decreases as T_i increases. Hence we assume

$$K(0, \dots, 0) = K_0 > 0, \quad \frac{\partial K}{\partial T_i} < 0 \quad \text{for } T_i > 0, \quad i = 1, 2, \dots, n. \quad (2.3)$$

Now we assume that the toxicity of each toxicant is different and it can be ordered, say the toxicant with concentration T_i is more toxic than the toxicant with concentration T_{i-1} , $i = 2, 3, \dots, n$. Hence if the biological species is exposed to each of the toxicants individually at some concentration $U_c > 0$ for the same time period t , then we have

$$r(0, \dots, 0, U_c) < r(0, \dots, 0, U_c, 0) < \dots < r(U_c, 0, \dots, 0) < r(0, \dots, 0) \quad \text{for some } U_c > 0. \quad (2.4)$$

Similarly if each of ^{the} toxicants is emitted into the environment individually with concentration T_c for the same duration t , we have the following relation for the respective carrying capacities,

$$K(0, \dots, 0, T_c) < K(0, \dots, 0, T_c, 0) < \dots < K(T_c, 0, \dots, 0) < K(0, \dots, 0) \quad \text{for some } T_c > 0. \quad (2.5)$$

In the following, we analyze the model (2.1) for $Q_i = 0$ and $Q_i = \text{a constant}$ for $i=1, 2, \dots, n$.

3. STABILITY ANALYSIS

3.1. THE CASE OF INSTANTANEOUS EMISSIONS

In this case, we consider

$$Q_i(t) = 0 \text{ and } T_i(t) = T_{i0} \quad \text{at } t = 0, i = 1, 2, \dots, n.$$

The model (2.1) has two nonnegative equilibria, namely $E_0(0, \dots, 0)$ and $E_1(K_0, 0, \dots, 0)$.

The local stability analysis of the equilibria can be studied by computing the variational matrices (Freedman, 1987) corresponding to each of the two equilibria. It can be noted that E_0 is a saddle point with unstable manifold in the N direction and with stable manifold in other directions. Using a quadratic Lyapunov's Function (La Salle and Lefschetz, 1961) it can also be seen that E_1 is locally asymptotically stable in N - T_i - U_i space. However, we can say much more about the stability of E_1 . In the following theorem, we show that E_1 is globally asymptotically stable.

THEOREM 3.1 If $N(0) > 0$, then E_1 is globally asymptotically stable.

Proof. From (2.1) we have

$$\begin{aligned} \frac{dN}{dt} &= r(U_1, \dots, U_n)N - \frac{r_0 N^2}{K(T_1, \dots, T_n)} \\ &\leq r_0 N - \frac{r_0 N^2}{K_0} \end{aligned}$$

hence $\limsup_{t \rightarrow \infty} N(t) \leq K_0$ for $N(0) < K_0$.

When $N(0) > K_0$, $\frac{dN}{dt}$ is negative for $t \geq 0$. Hence in this case also

$$\limsup_{t \rightarrow \infty} N(t) \leq K_0.$$

We also have

$$\sum_{i=1}^n \left(\frac{dT_i}{dt} + \frac{dU_i}{dt} \right) = - \sum_{i=1}^n \left(\delta_i T_i + \beta_i U_i + (1 - \pi_i) \nu_i N U_i \right)$$

$$\leq - \delta_0 \sum_{i=1}^n (T_i + U_i)$$

where $\delta_0 = \min_{1 \leq i \leq n} (\delta_i, \beta_i)$

This implies that

$$\sum_{i=1}^n \left(T_i(t) + U_i(t) \right) \leq \sum_{i=1}^n \left(T_i(0) + U_i(0) \right) e^{-\delta_0 t}$$

and hence $\lim_{t \rightarrow \infty} \sup T_i(t) = \lim_{t \rightarrow \infty} \sup U_i(t) = 0$, $i = 1, 2, \dots, n$.

This shows that the system is dissipative and in the limiting case, $N(t)$ is given by the solution of

$$\frac{dN}{dt} = r_0 N \left(1 - \frac{N}{K_0} \right)$$

Since $N(0) > 0$, the theorem follows.

This theorem implies that in the case of instantaneous spills of number of toxicants into the environment from different sources, the biological species with initial decrease in its density may recover back to its original carrying capacity but the time taken by this process may be large in comparison to the case of a single toxicant if the washout rates of toxicants are small.

3.2. THE CASE OF CONSTANT EMISSIONS

In this case we consider $Q_i(t) = Q_{i0} > 0$, $i = 1, 2, \dots, n$.

The model (2.1) has only two nonnegative equilibria, namely

$E_2(0, Q_{10}/\delta_1, \dots, Q_{n0}/\delta_n, 0, \dots, 0)$ and

$E^*(N^*, T_1^*, \dots, T_n^*, U_1^*, \dots, U_n^*)$. The existence of E_2 is obvious.

We show the existence of E^* as follows :

Here N^* , T_i^* , U_i^* are the positive solutions of the following system of algebraic equations :

$$N = r(U_1, \dots, U_n)K(T_1, \dots, T_n)/r_0 \quad (3.1a)$$

$$T_i = \frac{Q_{i0} + \pi_i \nu_i N U_i}{\delta_i + \alpha_i N} , \quad (3.1b)$$

$$U_i = \frac{\alpha_i T_i N}{\beta_i + \nu_i N} , \quad i = 1, 2, \dots, n. \quad (3.1c)$$

Since T_i and U_i decrease as Q_{i0} ($i = 1, 2, \dots, n$) increase, it is noted from (3.1a) that N decreases as the number of toxicants and/or their emission rates Q_{i0} increase.

Substituting T_i from (3.1b) in (3.1c), we get

$$U_i = \frac{\alpha_i Q_{i0} N}{f_i(N)} = h_i(N) \quad (\text{say}) \quad (3.2)$$

where

$$f_i(N) = \beta_i \delta_i + (\alpha_i \beta_i + \nu_i \delta_i)N + (1 - \pi_i) \alpha_i \nu_i N^2 > 0 \quad (3.3)$$

It is noted that U_i increases as Q_{i0} increases.

Substituting U_i from (3.2) in (3.1b), we get

$$T_i = g_i(N) \quad (3.4)$$

where

$$g_i(N) = \frac{Q_{i0} (\beta_i + \nu_i N)}{f_i(N)} \quad (3.5)$$

which increases as Q_{i0} increases.

Substituting U_i and T_i from (3.2) and (3.4) respectively in (3.1a), we get

$$r_0 N = r(h_1(N), h_2(N), \dots, h_n(N)) K(g_1(N), \dots, g_n(N)) \quad (3.6)$$

where

$$C_i = \frac{r_0 N^*}{K(T_1^*, \dots, T_n^*)} \frac{\partial K(T_1^*, \dots, T_n^*)}{\partial T_i},$$

$$D_i = \frac{r_0 N^*}{K(T_1^*, \dots, T_n^*)} \frac{\partial r(T_1^*, \dots, T_n^*)}{\partial U_i}, \quad i = 1, 2, \dots, n.$$

Then E^* is locally asymptotically stable.

Proof. Using the following positive definite function in the linearized form of (2.1),

$$V = \frac{1}{2N^*} (N - N^*)^2 + \frac{1}{2} \sum_{i=1}^n (T_i - T_i^*)^2 + \frac{1}{2} \sum_{i=1}^n (U_i - U_i^*)^2 \quad (3.9)$$

it can be checked that the derivative of V with respect to t under the conditions (3.8) is negative definite, proving the theorem.

Now to show that E^* is globally asymptotically stable, we first need a lemma which establishes a region of attraction for the system (2.1).

LEMMA 3.1 The set

$$\Omega_1 = \left\{ (N, T_i, U_i) : 0 \leq N \leq K_0, \quad 0 \leq \sum_{i=1}^n (T_i + U_i) \leq Q_0/\delta_0, \right.$$

$$\left. \text{where } \delta_0 = \min_{1 \leq i \leq n} (\delta_i, \beta_i), \quad Q_0 = \sum_{i=1}^n Q_{i0} \right\}$$

is a region of attraction for all solutions initiating in the positive orthant.

Proof. As in Theorem 3.1,

$$\limsup_{t \rightarrow \infty} N(t) \leq K_0$$

$$\text{and } \sum_{i=1}^n \left(\frac{dT_i}{dt} + \frac{dU_i}{dt} \right) \leq -\delta_0 \sum_{i=1}^n (T_i + U_i) + Q_0$$

Hence $\lim_{t \rightarrow \infty} \sup \sum_{i=1}^n (T_i(t) + U_i(t)) \leq Q_0/\delta_0$, proving the lemma.

THEOREM 3.3 In addition to the assumptions (2.2) and (2.3), let $r(U_1, \dots, U_n)$ and $K(T_1, \dots, T_n)$ satisfy the conditions

$$K_m \leq K(T_1, \dots, T_n) \leq K_0, \quad 0 \leq -\frac{\partial r}{\partial U_i} \leq \rho_i, \quad 0 \leq -\frac{\partial K}{\partial T_i} \leq k_i \quad (3.10)$$

in Ω_1 for all $T_i \geq 0$, $U_i \geq 0$ and for some positive constants K_m , ρ_i , k_i , $i = 1, 2, \dots, n$.

Then if the following inequalities hold

$$\left[\frac{r_0 k_i K_0}{K_m^2} + \frac{\alpha_i Q_0}{\delta_0} + \pi_i \nu_i U_i^* \right]^2 < \frac{1}{n} \frac{r_0}{K(T_1^*, \dots, T_n^*)} (\delta_i + \alpha_i N^*) \quad (3.11a)$$

$$\left[\rho_i + \frac{\nu_i Q_0}{\delta_0} + \alpha_i T_i^* \right]^2 < \frac{1}{n} \frac{r_0}{K(T_1^*, \dots, T_n^*)} (\beta_i + \nu_i N^*) \quad (3.11b)$$

$$\left[\pi_i \nu + \alpha_i \right]^2 K_0^2 < (\delta_i + \alpha_i N^*) (\beta_i + \nu_i N^*) \quad (3.11c)$$

$i = 1, 2, \dots, n$.

E^* is globally asymptotically stable with respect to all solutions initiating in the positive orthant.

PROOF :

Consider the following positive definite function about E^* ,

$$W = (N - N^* - N^* \ln \frac{N}{N^*}) + \frac{1}{2} \sum_{i=1}^n (T_i - T_i^*)^2 + \frac{1}{2} \sum_{i=1}^n (U_i - U_i^*)^2 \quad (3.12)$$

Differentiating W with respect to t along the solution of (2.1), we get

$$\begin{aligned}
\frac{dW}{dt} = & (N - N^*) \left[r(U_1, \dots, U_n) - \frac{r_0 N}{K(T_1, \dots, T_n)} \right] \\
& + \sum_{i=1}^n (T_i - T_i^*) \left[Q_i(t) - \delta_i T_i - \alpha_i T_i N + \pi_i \nu_i N U_i \right] \\
& + \sum_{i=1}^n (U_i - U_i^*) \left[-\beta_i U_i + \alpha_i T_i N - \nu_i N U_i \right]
\end{aligned} \tag{3.13}$$

A lengthy algebraic manipulation yields,

$$\begin{aligned}
\frac{dW}{dt} = & - \frac{r_0}{K(T_1^*, \dots, T_n^*)} (N - N^*)^2 - \sum_{i=1}^n (\delta_i + \alpha_i N^*) (T_i - T_i^*)^2 \\
& - \sum_{i=1}^n (\beta_i + \nu_i N^*) (U_i - U_i^*)^2 \\
& + \sum_{i=1}^n (N - N^*) (T_i - T_i^*) [-r_0 N Y_i - \alpha_i T_i + \pi_i \nu_i U_i^*] \\
& + \sum_{i=1}^n (N - N^*) (U_i - U_i^*) [X_i - \nu_i U_i + \alpha_i T_i^*] \\
& + \sum_{i=1}^n (T_i - T_i^*) (U_i - U_i^*) [\pi_i \nu_i N + \alpha_i N]
\end{aligned} \tag{3.14}$$

where

$$X_1 = \xi_1(U_1, \dots, U_n) \tag{3.15}$$

$$X_i = \xi_i(U_1^*, \dots, U_{i-1}^*, U_i, \dots, U_n), \quad i = 2, 3, \dots, n.$$

$$Y_1 = \eta_1(T_1, \dots, T_n) \tag{3.16}$$

$$Y_i = \eta_i(T_1^*, \dots, T_{i-1}^*, T_i, \dots, T_n), \quad i = 2, 3, \dots, n.$$

$$x_1 = \begin{cases} [r(U_1, U_2, \dots, U_n) - r(U_1^*, U_2, \dots, U_n)] / (U_1 - U_1^*), & U_1 \neq U_1^* \\ \frac{\partial r}{\partial U_1} (U_1^*, U_2, \dots, U_n), & U_1 = U_1^* \end{cases} \quad (3.17)$$

$$x_i = \begin{cases} [G_1 - H_1] / (U_i - U_i^*), & U_i \neq U_i^* \\ \frac{\partial r}{\partial U_i} (U_1^*, \dots, U_i^*, U_{i+1}, \dots, U_n), & U_i = U_i^* \end{cases} \quad (3.18)$$

where

$i = 2, 3, \dots, n.$

$$G_1 = r(U_1^*, \dots, U_{i-1}^*, U_i, \dots, U_n) \quad (3.19)$$

$$H_1 = r(U_1^*, \dots, U_i^*, U_{i+1}, \dots, U_n) \quad (3.20)$$

$$y_1 = \begin{cases} \left[\frac{1}{K(T_1, \dots, T_n)} - \frac{1}{K(T_1^*, T_2, \dots, T_n)} \right] / (T_1 - T_1^*), & T_1 \neq T_1^* \\ - \frac{\partial K}{\partial T_1} (T_1^*, T_2, \dots, T_n), & T_1 = T_1^* \end{cases} \quad (3.21)$$

$$y_i = \begin{cases} [G_2 - H_2] / (T_i - T_i^*), & T_i \neq T_i^* \\ - \frac{\partial K}{\partial T_i} (T_1^*, \dots, T_i^*, T_{i+1}, \dots, T_n), & T_i = T_i^* \end{cases} \quad (3.22)$$

where

$i = 2, 3, \dots, n.$

$$G_2 = \frac{1}{K(T_1^*, \dots, T_{i-1}^*, T_i, \dots, T_n)} \quad (3.23)$$

$$H_2 = \frac{1}{K(T_1^*, \dots, T_i^*, T_{i+1}, \dots, T_n)} \quad (3.24)$$

From (3.10) and mean value theorem we note that

$$|X_i| \leq \rho_i, \quad |Y_i| \leq k_i/K_m^2, \quad i = 1, 2, \dots, n. \quad (3.25)$$

From (3.14), $\frac{dW}{dt}$ can further be written as sum of the quadratics

$$\begin{aligned} \frac{dW}{dt} = & -\frac{1}{2} a_{111} (N - N^*)^2 + a_{121} (N - N^*) (T_1 - T_1^*) - \frac{1}{2} a_{221} (T_1 - T_1^*)^2 \\ & - \frac{1}{2} a_{111} (N - N^*)^2 + a_{122} (N - N^*) (T_2 - T_2^*) - \frac{1}{2} a_{222} (T_2 - T_2^*)^2 \\ & - \dots \dots \dots \\ & - \frac{1}{2} a_{111} (N - N^*)^2 + a_{12n} (N - N^*) (T_n - T_n^*) - \frac{1}{2} a_{22n} (T_n - T_n^*)^2 \\ & - \frac{1}{2} a_{111} (N - N^*)^2 + a_{131} (N - N^*) (U_1 - U_1^*) - \frac{1}{2} a_{331} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} a_{111} (N - N^*)^2 + a_{132} (N - N^*) (U_2 - U_2^*) - \frac{1}{2} a_{332} (U_2 - U_2^*)^2 \\ & - \dots \dots \dots \\ & - \frac{1}{2} a_{111} (N - N^*)^2 + a_{13n} (N - N^*) (U_n - U_n^*) - \frac{1}{2} a_{33n} (U_n - U_n^*)^2 \\ & - \frac{1}{2} a_{221} (T_1 - T_1^*)^2 + a_{231} (T_1 - T_1^*) (U_1 - U_1^*) - \frac{1}{2} a_{331} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} a_{222} (T_2 - T_2^*)^2 + a_{232} (T_2 - T_2^*) (U_2 - U_2^*) - \frac{1}{2} a_{332} (U_2 - U_2^*)^2 \\ & - \dots \dots \dots \\ & - \frac{1}{2} a_{22n} (T_n - T_n^*)^2 + a_{23n} (T_n - T_n^*) (U_n - U_n^*) - \frac{1}{2} a_{33n} (U_n - U_n^*)^2 \end{aligned} \quad (3.26)$$

where

$$a_{111} = \frac{1}{n} \frac{r_0}{K(T_1^*, \dots, T_n^*)}, \quad a_{22i} = (\delta_i + \alpha_i N^*), \quad a_{33i} = (\beta_i + \nu_i N^*),$$

$$a_{12i} = -r_0 N Y_i - \alpha_i T_i + \pi_i \nu_i U_i^*, \quad a_{13i} = X_i - \nu_i U_i + \alpha_i T_i^*,$$

$$a_{23i} = \pi_i \nu_i N + \alpha_i N.$$

$$i = 1, 2, \dots, n.$$

Then sufficient conditions for $\frac{dW}{dt}$ to be negative definite are that the following inequalities hold :

$$a_{12i}^2 < a_{11i} a_{22i} \quad (3.27)$$

$$a_{13i}^2 < a_{11i} a_{33i} \quad (3.28)$$

$$a_{23i}^2 < a_{22i} a_{33i} \quad (3.29)$$

We note that (3.11a) \Rightarrow (3.27), (3.11b) \Rightarrow (3.28) and (3.11c) \Rightarrow (3.29). Hence from Lyapunov's theorem of stability (La Salle and Lefschetz, 1961) we conclude that W is a Lyapunov function with respect to E^* whose domain contains the region of attraction Ω_1 , proving the theorem.

It may be noted here that when the conditions (3.11) are satisfied (i.e. the positive equilibrium E^* is globally asymptotically stable), the conditions for local stability of this equilibrium i.e. the conditions (3.8) are also satisfied.

The above theorems imply that if the toxicants are emitted into the environment with constant rates, the equilibrium level of population decreases considerably. It is noted here that if the number of toxicants, their toxicity and influx rates into the environment increase, the species density decreases further and it may even tend to zero sooner than the case of a single toxicant, other parameters being the same in the system.

4. SOME REMARKS : i). When $Q_i(t) = 0$ for some i , then the corresponding model can be analyzed as in case II and the stability results are found to be similar to this case. In particular, in this case it may be noted that the equilibrium level of the population is higher than the case II, for the same values of parameters, and is stable under suitably modified conditions similar to (3.11).

ii). In the present Chapter, we have taken all the toxicants to be emitted in to the environment by some external sources, however, we can also take some of the toxicants being produced by the biological species and the rest by some external sources. The problem is still open but can be analyzed by following the procedure as given in Chapter III.

iii). If one of the toxicants is a secondary toxicant, the corresponding model can be proposed and analyzed as in Chapter IV.

5. CONCLUSIONS

In this Chapter, we have presented a mathematical model for studying the simultaneous effects of a number of toxicants (pollutants) emitted into the environment on a biological population. The cases of instantaneous spills and constant emissions of these toxicants have been considered and the existence of non trivial equilibrium has been proved. It has been shown that in the case of instantaneous spills, toxicants from the environment washout completely and the population may recover back to its initial carrying capacity, the duration being dependent upon the number of toxicants and their toxicity, influx and washout rates.

In the case of constant emissions of these toxicants, it has been shown that the population settles down to an equilibrium level, which is much lower than its initial (toxicant independent) carrying capacity, the magnitude of which depends upon the number of toxicants emitted into the environment, their toxicity, emission and washout rates. It has also been noted that in the case of uncontrolled continuous emissions of toxicants with large influx rates, the affected biological population may be doomed to extinction sooner than the case of a single toxicant, other parameters in the system being the same. It is also pointed out here that as the number of toxicants and their toxicity increase, the density of the affected population decreases further.

CHAPTER VI

ALLELOPATHIC EFFECTS BETWEEN TWO COMPETING BIOLOGICAL SPECIES

1. INTRODUCTION

Plants in their habitats, live in specific communities interacting with each other. It had been observed that some plant species produce volatile chemical compounds (toxicants) which inhibit the growth of other plants in the neighboring area. Rice (1984) termed this phenomenon as allelopathy. According to him, "Any direct or indirect inhibitory or stimulatory effect of one plant on another through the production of volatile chemical compounds may be termed as allelopathy". Different types of organic compounds (toxicants) have been identified as allelochemicals (Grummer, 1955, 1961).

Various experimental researches have been conducted to study the phenomenon of allelopathy and it has been noted that plant roots play an important role in producing growth inhibitory toxicants (Das and Sadhu, 1985; Grab, 1961; Mandal *et al*, 1996). Although the quantity of the toxicants liberated by the plant roots is not very large, it is enough to exert a strong influence on the soil microflora and to affect significantly the growth of the neighboring plants.

Jay Kumar *et al* (1987 a,b) have observed the allelopathic effects of teak leaf extract and bamboo root extract on the growth of groundnut and corn seedlings. Eyini *et al* (1989) found that water extract of the fallen leaves of bamboo tree inhibited the

growth of groundnut seedlings.

Although, a number of experiments have been conducted to observe the allelopathic effects (Grummer, 1961; Lee and Monsi, 1963; Keating, 1977; Basu et al, 1987; Abdul - Rahman and Habib, 1989; Zackrisson and Nilsson, 1992; Frank, 1994; Gallet, 1994; Inderjit and Dakshini, 1994; Chung and Miller, 1995), very little attention has been paid to model this vital phenomenon mathematically (Mandal et al, 1995; Durrett and Levin, 1997; Mandal and Tapaswi, 1997; Mukhopadhyay et al, 1998). Therefore, in this Chapter, a mathematical model has been proposed to study the allelopathic effects between two competing biological species (such as plant species) using nonlinear differential equations (Maynard - Smith, 1974).

It has been assumed that both the species follow logistic growth (Freedman and Shukla, 1991) in absence of the other species. The model has been analyzed using stability theory.

2. MATHEMATICAL MODEL

Let N_1 be the biomass density of the first species which is producing toxicant and N_2 be that of the affected species (we call it as second species). Let T be the concentration of the toxicant produced by the first species, present in the environment and U be the concentration of the toxicant uptaken by the second species. It is assumed that both the species compete with each other and hence their growth are decreased in the presence of each other. Let $r_1(N_2)$ and $r_2(U, N_1)$ are their specific growth rate functions and K_1 and $K_2(T)$ be their respective carrying capacities with respect to

the environment.

In view of the above, the model is proposed as follows:

$$\begin{aligned}
 \frac{dN_1}{dt} &= r_1(N_2)N_1 - r_{10} \frac{N_1^2}{K_1} \\
 \frac{dN_2}{dt} &= r_2(U, N_1)N_2 - r_{20} \frac{N_2^2}{K(T)} \\
 \frac{dT}{dt} &= \lambda N_1 - \delta_0 T - \alpha N_2 T + \pi \nu N_2 U + \theta_1 \delta_1 U \\
 \frac{dU}{dt} &= -\delta_1 U + \alpha N_2 T - \nu N_2 U + \theta_0 \delta_0 T
 \end{aligned} \tag{2.1}$$

where

$$\begin{aligned}
 N_1(0) = N_{10} \geq 0, \quad N_2(0) = N_{20} \geq 0, \quad T(0) = T_0 = cN_{10} \geq 0, \quad U(0) = c_1 T_0, \\
 c > 0, \quad c_1 > 0, \quad 0 \leq \theta_0 \leq 1, \quad 0 \leq \theta_1 \leq 1, \quad 0 \leq \pi \leq 1.
 \end{aligned}$$

In above model (2.1), it is assumed that the rate of toxicant, produced in the environment, is proportional to the biomass density $N_1(t)$ of the first species. Thus, we assume that $\lambda N_1(t)$ is the emission rate of toxicant being produced by the first species (λ being a positive constant). The environmental concentration of the toxicant, $T(t)$ is assumed to decrease due to its uptake by the second species with rate " $\alpha N_2 T$ " (α is a positive constant). The positive constant δ_0 is the depletion rate coefficient of toxicant from the environment due to some natural factors and a fraction θ_0 of it may be uptaken by the affected species through the food chain. The constant $\delta_1 > 0$ is the natural depletion rate coefficient of $U(t)$ and a fraction θ_1 of it may reenter in to environment due to recycling and thus increasing the environmental concentration of the toxicant. Similarly, due to dying out of some

members of the second species, the uptake concentration in the second species may decrease with the rate $\nu N_2 U$ and a fraction π of which may reenter into the environment. c, c_1 are positive constants.

In the model (2.1), the growth rate functions $r_1(N_2)$ and $r_2(U, N_1)$ are assumed to satisfy the following properties,

$$r_1(0) = r_{10} > 0, r_1'(N_2) < 0 \text{ for all } N_2 > 0 \quad (2.2a)$$

$$r_2(0,0) = r_{20} > 0, \frac{\partial r_2(U, N_1)}{\partial U} < 0, \frac{\partial r_2(U, N_1)}{\partial N_1} < 0 \text{ for } U, N_1 > 0 \quad (2.2b)$$

Also in the model (2.1), the function $K_2(T)$ denotes the maximum biomass density of the second species which the environment can support in the presence of toxicant and it is assumed to satisfy the following property,

$$K_2(0) = K_{20} > 0, K_2'(T) < 0 \text{ for all } T > 0 \quad (2.2c)$$

The carrying capacity of the toxicant producing species is K_1 and is assumed to be a constant.

Now we analyze model (2.1) under the above assumptions.

3. MATHEMATICAL ANALYSIS

The model (2.1) has four equilibrium points, namely:

$$E_1 = (0, 0, 0, 0), \quad E_2 = (0, K_{20}, 0, 0),$$

$$E_3 = (K_1, 0, \frac{\lambda K_1}{\delta_0(1-\theta_0\theta_1)}, \frac{\lambda K_1\theta_0}{\delta_1(1-\theta_0\theta_1)}) \text{ and } E_4 = (N_1^*, N_2^*, T^*, U^*).$$

The existence of E_1, E_2 and E_3 can be shown easily. However the existence of E_4 is not so obvious, therefore in the following, its existence has been proved.

We note that N_1^* , N_2^* , T^* and U^* are the positive solutions of the following algebraic equations:

$$N_1 = K_1 r_1(N_2)/r_{10} = h_1(N_2) \quad (\text{say}) \quad (3.1a)$$

$$N_2 = r_2(U, N_1) K_2(T)/r_{20} = h_2(N_2) \quad (\text{say}) \quad (3.1b)$$

where

$$T = \frac{\lambda(\delta_1 + \nu N_2) h_1(N_2)}{f(N_2)} = h(N_2) \quad (\text{say}) \quad (3.1c)$$

$$U = \frac{\lambda(\theta_0 \delta_0 + \alpha N_2) h_1(N_2)}{f(N_2)} = g(N_2) \quad (\text{say}) \quad (3.1d)$$

$$\begin{aligned} \text{and } f(N_2) &= \delta_0 \delta_1 (1 - \theta_0 \theta_1) + \delta_1 \alpha (1 - \theta_1) N_2 + \delta_0 \nu (1 - \pi \theta_0) N_2 \\ &\quad + \nu \alpha (1 - \pi) N_2^2 \end{aligned} \quad (3.1e)$$

We note that $h_1(N_2) > 0$, $h_2(N_2) > 0$ and $\frac{dh_1}{dN_2} < 0$

It is also noted from (3.1c) and (3.1d) that T and U increase as λ increases. Hence $r_2(U, N_1)$ and $K_2(T)$ decrease as λ increases and thus decreasing N_2^* . Now taking

$$F(N_2) = r_{20} N_2 - r_2(g(N_2), h_1(N_2)) K_2(h(N_2)), \quad (3.2a)$$

We note that $F(0) < 0$ and $F(K_{20}) > 0$. This shows that the equation $F(N_2) = 0$ has a root say N_2^* in the interval $0 < N_2^* < K_{20}$. For the uniqueness of N_2^* , we must have $F'(N_2) > 0$ in the interval $0 < N_2 < K_{20}$, i.e.

$$\begin{aligned} \frac{dF}{dN_2} &= r_{20} - r_2(g(N_2), h_1(N_2)) \frac{dK_2}{dT} \frac{dh}{dN_2} \\ &\quad - K_2(h(N_2)) \left\{ \frac{\partial r_2}{\partial U} \frac{dg}{dN_2} + \frac{\partial r_2}{\partial N_1} \frac{dh_1}{dN_2} \right\} > 0 \end{aligned} \quad (3.2b)$$

Knowing the value of N_2^* , the values of N_1^* , T^* and U^* can be computed using equations (3.1a), (3.1c) and (3.1d) respectively.

The local stability behavior of the equilibria E_1 , E_2 and E_3 can be seen by computing variational matrices corresponding to them. The variational matrix for the model (2.1) is given by

$$M = \begin{bmatrix} r_1(N_2) - \frac{2r_{10}N_1}{K_1} & r_1'(N_2)N_1 & 0 & 0 \\ \frac{\partial r_2}{\partial N_1} N_2 & r_2(U, N_1) - \frac{2r_{20}N_2}{K_2(T)} & r_{20}N_2^2 \frac{K_2'(T)}{K_2^2(T)} & \frac{\partial r_2}{\partial U} N_2 \\ \lambda & -\alpha T + \pi\nu U & -(\delta_0 + \alpha N_2) & \theta_1\delta_1 + \pi\nu N_2 \\ 0 & \alpha T - \nu U & \theta_0\delta_0 + \alpha N_2 & -(\delta_1 + \nu N_2) \end{bmatrix}$$

Now

$$M_1 = M|_{E_1} = \begin{bmatrix} r_{10} & 0 & 0 & 0 \\ 0 & r_{20} & 0 & 0 \\ \lambda & 0 & -\delta_0 & \theta_1\delta_1 \\ 0 & 0 & \theta_0\delta_0 & -\delta_1 \end{bmatrix},$$

$$M_2 = M|_{E_2} = \begin{bmatrix} r_1(K_{20}) & 0 & 0 & 0 \\ K_{20} \frac{\partial r_2}{\partial N_1}(0,0) - r_{20} & r_{20}K_2'(0) & K_{20} \frac{\partial r_2}{\partial U}(0,0) & \\ \lambda & 0 & -(\delta_0 + \alpha K_{20}) & \theta_1\delta_1 + \pi\nu K_{20} \\ 0 & 0 & \theta_0\delta_0 + \alpha K_{20} & -(\delta_1 + \nu K_{20}) \end{bmatrix},$$

$$M_3 = M|_{E_3} = \begin{bmatrix} -r_{10} & K_1 r'_1(0) & 0 & 0 \\ 0 & r_2 \left(\frac{\lambda K_1 \theta_0}{\delta_1 (1 - \theta_0 \theta_1)} , N_1 \right) & 0 & 0 \\ \lambda & \frac{\lambda K_1}{(1 - \theta_0 \theta_1)} \left(-\frac{\alpha}{\delta_0} + \frac{\pi \nu \theta_0}{\delta_1} \right) & -\delta_0 & \theta_1 \delta_1 \\ 0 & \frac{\lambda K_1}{(1 - \theta_0 \theta_1)} \left(\frac{\alpha}{\delta_0} - \frac{\nu \theta_0}{\delta_1} \right) & \theta_0 \delta_0 & -\delta_1 \end{bmatrix}$$

From the above, it follows that E_1 is a saddle point whose stable manifold is locally in the T-U plane and unstable manifold is locally in the N_1 - N_2 plane. E_2 is also a saddle point with stable manifold locally in the N_2 -T-U space and unstable manifold locally in the N_1 direction. E_3 is also a saddle point with stable manifold locally in the N_1 -T-U space and unstable manifold locally in the N_2 direction.

The stability behavior of E_4 from the corresponding matrix is not obvious. In the following theorem, therefore, the local stability behavior of E_4 is established by using Lyapunov's stability method.

THEOREM 3.1 Let the following inequalities hold :

$$\left[r'_1(N_2^*) + \frac{\partial r_2}{\partial N_1}(U^*, N_1^*) \right]^2 < \frac{2}{3} \frac{r_{10}}{K_1} \frac{r_{20}}{K_2(T^*)} \quad (3.3a)$$

$$\lambda^2 < \frac{2}{3} \frac{r_{10}}{K_1} (\delta_0 + \alpha N_2^*) \quad (3.3b)$$

$$\left[r_{20} N_2^* \frac{K_2'(T^*)}{K_2^2(T^*)} - (\alpha T^* + \pi \nu U^*) \right]^2 < \frac{4}{9} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha N_2^*) \quad (3.3c)$$

$$\left[\frac{\partial r_2}{\partial U}(U^*, N_1^*) + (\alpha T^* - \nu U^*) \right]^2 < \frac{2}{3} \frac{r_{20}}{K_2(T^*)} (\delta_1 + \nu N_2^*) \quad (3.3d)$$

$$\left[(\theta_1 \delta_1 + \pi \nu N_2^*) + (\theta_0 \delta_0 + \alpha N_2^*) \right]^2 < \frac{2}{3} (\delta_0 + \alpha N_2^*) (\delta_1 + \nu N_2^*) \quad (3.3e)$$

then E_4 is locally asymptotically stable.

PROOF: Linearizing the model (2.1) by substituting

$$N_1 = N_1^* + n_1, \quad N_2 = N_2^* + n_2, \quad T = T^* + \tau \quad \text{and} \quad U = U^* + u, \quad (3.4a)$$

we get

$$\frac{dn_1}{dt} = - \frac{r_{10}}{K_1} N_1^* n_1 + \left(r_1'(N_2^*) N_1^* \right) n_2$$

$$\begin{aligned} \frac{dn_2}{dt} = & \left(\frac{\partial r_2}{\partial N_1^*} N_2^* \right) n_1 + \left(- r_{20} \frac{N_2^*}{K_2(T^*)} \right) n_2 + \left(r_{20} N_2^{*2} \frac{K_2'(T^*)}{K_2^2(T^*)} \right) \tau \\ & + \left(\frac{\partial r_2}{\partial U^*} N_2^* \right) u \end{aligned}$$

$$\frac{d\tau}{dt} = \lambda n_1 + (-\alpha T^* + \pi \nu U^*) n_2 - (\delta_0 + \alpha N_2^*) \tau + (\theta_1 \delta_1 + \pi \nu N_2^*) u$$

$$\frac{du}{dt} = (\alpha T^* - \nu U^*) n_2 + (\theta_0 \delta_0 + \alpha N_2^*) \tau - (\delta_1 + \nu N_2^*) u \quad (3.5)$$

Using the following positive definite function

$$V = \frac{1}{2N_1^*} n_1^2 + \frac{1}{2N_2^*} n_2^2 + \frac{c_1}{2} \tau^2 + u^2 \quad (3.6a)$$

Differentiating V with respect to t , using (3.5) and after simplifying, we get

$$\begin{aligned}
\frac{dV}{dt} = & -\frac{1}{2} a_{11}n_1^2 + a_{12}n_1n_2 - \frac{1}{2} a_{22}n_2^2 \\
& - \frac{1}{2} a_{11}n_1^2 + a_{13}n_1\tau - \frac{1}{2} a_{33}\tau^2 \\
& - \frac{1}{2} a_{22}n_2^2 + a_{23}n_2\tau - \frac{1}{2} a_{33}\tau^2 \\
& - \frac{1}{2} a_{22}n_2^2 + a_{24}n_2u - \frac{1}{2} a_{44}u^2 \\
& - \frac{1}{2} a_{33}\tau^2 + a_{34}\tau u - \frac{1}{2} a_{44}u^2
\end{aligned} \tag{3.6b}$$

where

$$\begin{aligned}
a_{11} &= \frac{r_{10}}{K_1}, \quad a_{22} = \frac{2}{3} \frac{r_{20}}{K_2(T^*)}, \quad a_{33} = \frac{2}{3} (\delta_0 + \alpha N_2^*), \\
a_{44} &= (\delta_1 + \nu N_2^*), \quad a_{12} = r_1'(N_2^*) + \frac{\partial r_2}{\partial N_1}(U^*, N_1^*), \\
a_{23} &= r_{20}N_2^* \frac{K_2'(T^*)}{K_2^2(T^*)} - (\alpha T^* - \pi \nu U^*), \quad a_{13} = \lambda, \\
a_{24} &= \frac{\partial r_2}{\partial U}(U^*, N_1^*) + (\alpha T^* - \nu U^*), \\
a_{34} &= (\theta_1 \delta_1 + \pi \nu N_2^*) + (\theta_0 \delta_0 + \alpha N_2^*)
\end{aligned} \tag{3.6c}$$

Thus $\frac{dV}{dt}$ will be negative definite provided

$$\begin{aligned}
a_{12}^2 &< a_{11}a_{22}, \quad a_{13}^2 < a_{11}a_{33}, \quad a_{23}^2 < a_{22}a_{33}, \quad a_{24}^2 < a_{22}a_{44} \\
\text{and } a_{34}^2 &< a_{33}a_{44},
\end{aligned}$$

which give the same inequalities as in equations (3.3a-e).

The following theorem characterizes the global stability behavior of the equilibrium point E_4 . For this, we need the following lemma, which gives a region of attraction for all

solutions of the system (2.1) initiating in the interior of the positive orthant.

LEMMA 3.1: The region

$$\Omega = \left\{ (N_1, N_2, T, U) : 0 \leq N_1 \leq K_1, 0 \leq N_2 \leq K_{20}, 0 \leq T + U \leq \frac{\lambda K_1}{\delta} \right\}$$

attracts all solutions initiating in the interior of the positive orthant, where

$$\delta = \min \{ \delta_0(1 - \theta_0), \delta_1(1 - \theta_1) \}.$$

PROOF: From the first equation of (2.1), we have

$$\frac{dN_1}{dt} \leq r_1(0)N_1 - r_{10} \frac{N_1^2}{K_1} = r_{10}N_1 \left(1 - \frac{N_1}{K_1}\right)$$

Thus, $\limsup_{t \rightarrow \infty} N_1(t) \leq K_1$.

From the second equation of (2.1), we have

$$\frac{dN_2}{dt} \leq r_{20}N_2 \left(1 - \frac{N_2}{K_{20}}\right)$$

$$\Rightarrow \limsup_{t \rightarrow \infty} N_2(t) \leq K_{20}.$$

Adding last two equations of (2.1), we get

$$\frac{dT}{dt} + \frac{dU}{dt} \leq \lambda K_1 - \delta(T + U),$$

$$\text{where } \delta = \min \{ \delta_0(1 - \theta_0), \delta_1(1 - \theta_1) \}$$

which gives $\limsup_{t \rightarrow \infty} [T(t) + U(t)] \leq \frac{\lambda K_1}{\delta}$, proving the lemma.

THEOREM 3.2 In addition to the assumption (2.2a) - (2.2c), let the functions $r_1(N_2)$, $r_2(U, N_1)$ and $K_2(T)$ satisfy in Ω

$$\left| r'_1(N_2) \right| \leq \rho_{12}, \quad \left| \frac{\partial r_2}{\partial N_1}(U^*, N_1) \right| \leq \rho_{21}, \quad \left| \frac{\partial r_2}{\partial U}(U, N_1) \right| \leq \rho_{22},$$

$$K_m \leq K_2(T) \leq K_{20}, \quad \left| K'_2(T) \right| \leq k,$$

where ρ_{12} , ρ_{21} , ρ_{22} , K_m and k are positive constants. Then if the following inequalities hold

$$[\rho_{12} + \rho_{21}]^2 < \frac{2}{3} \frac{r_{10}}{K_1} \frac{r_{20}}{K_2(T^*)} \quad (3.7a)$$

$$\lambda^2 < \frac{2}{3} \frac{r_{10}}{K_1} (\delta_0 + \alpha N_2^*) \quad (3.7b)$$

$$\left[\frac{r_{20} K_{20}}{K_m^2} k + \frac{\alpha \lambda K_1}{\delta} + \pi \nu U^* \right]^2 < \frac{4}{9} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha N_2^*) \quad (3.7c)$$

$$\left[\rho_{22} + \alpha T^* + \frac{\nu \lambda K_1}{\delta} \right]^2 < \frac{2}{3} \frac{r_{20}}{K_2(T^*)} (\delta_1 + \nu N_2^*) \quad (3.7d)$$

$$\left[(\theta_1 \delta_1 + \pi \nu K_{20}) + (\theta_0 \delta_0 + \alpha K_{20}) \right]^2 < \frac{2}{3} (\delta_0 + \alpha N_2^*) (\delta_1 + \nu N_2^*) \quad (3.7e)$$

E_4 is globally asymptotically stable with respect to all solutions initiating in the interior of the positive orthant.

PROOF : Consider the following positive definite function around E_4 ,

$$\begin{aligned} W(N_1, N_2, T, U) = & \left\{ N_1 - N_1^* - N_1^* \ln \frac{N_1}{N_1^*} \right\} + \left\{ N_2 - N_2^* - N_2^* \ln \frac{N_2}{N_2^*} \right\} \\ & + \frac{1}{2} (T - T^*)^2 + \frac{1}{2} (U - U^*)^2 \end{aligned} \quad (3.8a)$$

The derivative of W with respect to t , along the solutions of the system (2.1) is given by

$$\frac{dW}{dt} = (N_1 - N_1^*) \frac{\dot{N}_1}{N_1} + (N_2 - N_2^*) \frac{\dot{N}_2}{N_2} + (T - T^*) \dot{T} + (U - U^*) \dot{U}$$

Substituting the values of \dot{N}_1 , \dot{N}_2 , \dot{T} and \dot{U} from equations (2.1) in the above, we get after a little algebraic manipulation

$$\begin{aligned}
\frac{dW}{dt} = & - \frac{r_{10}}{K_1} (N_1 - N_1^*)^2 - \frac{r_{20}}{K_2(T^*)} (N_2 - N_2^*)^2 \\
& - (\delta_0 + \alpha N_2^*) (T - T^*)^2 - (\delta_1 + \nu N_2^*) (U - U^*)^2 \\
& + (N_1 - N_1^*) (N_2 - N_2^*) \left\{ \xi_1(N_2) + \xi_{21}(U^*, N_1) \right\} \\
& + (N_1 - N_1^*) (T - T^*) \lambda \\
& + (N_2 - N_2^*) (T - T^*) \left\{ -r_{20} N_2 \eta(T) - \alpha T + \pi \nu U^* \right\} \\
& + (N_2 - N_2^*) (U - U^*) \left\{ \xi_{22}(U, N_1) + \alpha T^* - \nu U \right\} \\
& + (T - T^*) (U - U^*) \left\{ (\pi \nu N_2 + \theta_1 \delta_1) + (\alpha N_2 + \theta_0 \delta_0) \right\} \quad (3.8b)
\end{aligned}$$

where

$$\xi_1(N_2) = \begin{cases} \frac{r_1(N_2) - r_1(N_2^*)}{(N_2 - N_2^*)} & , N_2 \neq N_2^* \\ r_1'(N_2^*) & , N_2 = N_2^* \end{cases} \quad (3.9a)$$

$$\xi_{21}(U^*, N_1) = \begin{cases} \frac{r_2(U^*, N_1) - r_2(U^*, N_1^*)}{(N_1 - N_1^*)} & , N_1 \neq N_1^* \\ \frac{\partial r_2}{\partial N_1}(U^*, N_1^*) & , N_1 = N_1^* \end{cases} \quad (3.9b)$$

$$\xi_{22}(U, N_1) = \begin{cases} \frac{r_2(U, N_1) - r_2(U^*, N_1)}{(U - U^*)} & , U \neq U^* \\ \frac{\partial r_2}{\partial U}(U^*, N_1) & , U = U^* \end{cases} \quad (3.9c)$$

and

$$\eta(T) = \begin{cases} \frac{\frac{1}{K_2(T)} - \frac{1}{K_2(T^*)}}{(T - T^*)} & , T \neq T^* \\ -\frac{K_2'(T^*)}{K_2^2(T^*)} & , T = T^* \end{cases} \quad (3.9d)$$

Thus $\frac{dW}{dt}$ can further be written as sum of the quadratics

$$\begin{aligned} \frac{dW}{dt} = & -\frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{12} (N_1 - N_1^*) (N_2 - N_2^*) - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 \\ & - \frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{13} (N_1 - N_1^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{23} (N_2 - N_2^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{24} (N_2 - N_2^*) (U - U^*) - \frac{1}{2} b_{44} (U - U^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{34} (T - T^*) (U - U^*) - \frac{1}{2} b_{44} (U - U^*)^2 \end{aligned} \quad (3.10a)$$

where

$$b_{11} = \frac{r_{10}}{K_1}, \quad b_{22} = \frac{2}{3} \frac{r_{20}}{K_2(T^*)}, \quad b_{33} = \frac{2}{3} (\delta_0 + \alpha N_2^*),$$

$$b_{44} = (\delta_1 + \nu N_2^*), \quad b_{12} = \xi_1(N_2) + \xi_{21}(U^*, N_1),$$

$$b_{23} = -r_{20} N_2 \eta(T) - \alpha T + \pi \nu U^*, \quad b_{13} = \lambda,$$

$$b_{24} = \xi_{22}(U, N_1) + \alpha T^* - \nu U, \quad b_{34} = (\pi \nu N_2 + \theta_1 \delta_1) + (\alpha N_2 + \theta_0 \delta_0) \quad (3.10b)$$

Thus $\frac{dW}{dt}$ will be negative definite provided

$$b_{12}^2 < b_{11} b_{22}, \quad b_{13}^2 < b_{11} b_{33}, \quad b_{23}^2 < b_{22} b_{33}, \quad b_{24}^2 < b_{22} b_{44}$$

and $b_{34}^2 < b_{33} b_{44}$, which give the same inequalities as given in (3.7a-e).

Hence W is a Lyapunov's function with respect to E_4 whose domain contains Ω and therefore E_4 is globally asymptotically stable and hence the theorem.

The above theorems imply that under certain conditions, the equilibrium density of the species affected by the toxicant, decreases. The amount of decrease depends upon the rate of production of the toxicant by the other species and the biomass density of this species. They also suggest that for large production rate of the toxicant, the affected species may be doomed to extinction.

4. A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANTS

In this case, we assume that the dynamics of the environmental and uptake concentrations of the toxicant are so fast such that their equilibria are attained with the densities of both the biological species almost instantaneously. In such a case, we assume :

$$\frac{dT}{dt} \approx 0 \quad \text{and} \quad \frac{dU}{dt} \approx 0 \quad \text{for all } t \geq 0.$$

We have from last two equations of (2.1)

$$T \approx \frac{\lambda(\delta_1 + \nu N_2)h_1(N_2)}{f(N_2)} = h(N_2) \quad (\text{say}) \quad (4.1a)$$

$$U \approx \frac{\lambda(\theta_0\delta_0 + \alpha N_2)h_1(N_2)}{f(N_2)} = g(N_2) \quad (\text{say}) \quad (4.1b)$$

where $h_1(N_2)$ and $f(N_2)$ are same as defined by (3.1a) and (3.1e) respectively. We note that T and U are expressed as functions of N_2 . Then the model (2.1) is reduced to a two dimensional form and

$r_2(U, N_1)$ and $K_2(T)$ are now functions of N_2 through (4.1a-b). They also decrease as λ increases and hence $r_2(U(N_2), N_1)$ and $K_2(T(N_2))$ decrease with λ .

The model can finally be written as:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1(N_2)N_1 - r_{10} \frac{N_1^2}{K_1} \\ \frac{dN_2}{dt} &= r_2(U(N_2), N_1)N_2 - r_{20} \frac{N_2^2}{K_2(T(N_2))}\end{aligned}\quad (4.2)$$

with $N_i(0) = N_{i0} \geq 0$, $i = 1, 2$.

The above model (4.2), is a generalized Volterra type competition model where growth rate and carrying capacities are functions of population densities.

To analyze the model (4.2), we note that it has four equilibrium points namely $E_5 = (0, 0)$, $E_6 = (K_1, 0)$, $E_7 = (0, \hat{N}_2)$ and $E_8 = (\tilde{N}_1, \tilde{N}_2)$ where \hat{N}_2 is the solution of

$$r_{20}N_2 - r_2(g(N_2), 0)K_2(h(N_2)) = 0 \quad (4.3a)$$

and \tilde{N}_2 is the solution of

$$r_{20}N_2 - r_2(g(N_2), h_1(N_2))K_2(h(N_2)) = 0 \quad (4.3b)$$

Knowing the value of \tilde{N}_2 , \tilde{N}_1 can be computed from (3.1a).

The existence and uniqueness of \hat{N}_2 and \tilde{N}_2 can be proved as in previous section.

We also note that $\tilde{N}_2 < K_{20}$, $\tilde{N}_1 < K_1$, $\tilde{N}_2 < K_{20}$ and \tilde{N}_2 , \tilde{N}_1 , \tilde{N}_2 decrease as λ increases and may even tend to zero for large λ .

To show the global stability behavior of E_8 we consider the following positive definite function around E_8 :

$$V_1(N_1, N_2) = (N_1 - \tilde{N}_1 - \tilde{N}_1 \ln \frac{N_1}{\tilde{N}_1}) + (N_2 - \tilde{N}_2 - \tilde{N}_2 \ln \frac{N_2}{\tilde{N}_2})$$

Differentiating V_1 with respect to t along the solution of the model (4.2), we get

$$\begin{aligned}
 \frac{dV_1}{dt} &= (N_1 - \tilde{N}_1) \left[r_1(N_2) - r_{10} \frac{N_1}{K_1} \right] \\
 &+ (N_2 - \tilde{N}_2) \left[r_2(U(N_2), N_1) - r_{20} \frac{N_2}{K_2(T(N_2))} \right] \\
 &= (N_1 - \tilde{N}_1) \left[r_1(N_2) - r_1(\tilde{N}_2) - \frac{r_{10}}{K_1} (N_1 - \tilde{N}_1) \right] \\
 &+ (N_2 - \tilde{N}_2) \left[r_2(U(N_2), N_1) - r_2(U(\tilde{N}_2), N_1) + r_2(U(\tilde{N}_2), N_1) \right. \\
 &- r_2(U(\tilde{N}_2), \tilde{N}_1) - \frac{r_{20} N_2}{K_2(T(N_2))} + \frac{r_{20} N_2}{K_2(T(\tilde{N}_2))} - \frac{r_{20} N_2}{K_2(T(\tilde{N}_2))} \\
 &\left. + \frac{r_{20} \tilde{N}_2}{K_2(T(\tilde{N}_2))} \right] \\
 &= - \frac{r_{10}}{K_1} (N_1 - \tilde{N}_1)^2 \\
 &+ (N_2 - \tilde{N}_2)^2 \left[\chi_{22}(N_1, N_2) - r_{20} N_2 \eta_{22}(N_2) - \frac{r_{20}}{K_2(T(\tilde{N}_2))} \right] \\
 &+ (N_1 - \tilde{N}_1) (N_2 - \tilde{N}_2) \left[\chi_{12}(N_2) + \chi_{21}(N_1, \tilde{N}_2) \right] \tag{4.4}
 \end{aligned}$$

where

$$\chi_{12}(N_2) = \begin{cases} [r_1(N_2) - r_1(\tilde{N}_2)] / (N_2 - \tilde{N}_2) & , \quad N_2 \neq \tilde{N}_2 \\ \left. \frac{dr_1}{dN_2} \right|_{N_2 = \tilde{N}_2} & , \quad N_2 = \tilde{N}_2 \end{cases}$$

$$\chi_{22}(N_1, N_2) = \begin{cases} [r_2(U(N_2), N_1) - r_2(U(\tilde{N}_2), N_1)] / (N_2 - \tilde{N}_2), & N_2 \neq \tilde{N}_2 \\ \left. \frac{\partial r_2}{\partial U}(U(N_2), N_1) \frac{dU}{dN_2} \right|_{N_2 = \tilde{N}_2} & , \quad N_2 = \tilde{N}_2 \end{cases}$$

$$\chi_{21}(N_1, \tilde{N}_2) = \begin{cases} [r_2(U(\tilde{N}_2), N_1) - r_2(U(\tilde{N}_2), \tilde{N}_1)] / (N_1 - \tilde{N}_1), & N_1 \neq \tilde{N}_1 \\ \left. \frac{\partial r_2}{\partial N_1}(U(\tilde{N}_2), N_1) \right|_{N_1 = \tilde{N}_1} & , \quad N_1 = \tilde{N}_1 \end{cases}$$

$$\eta_{22}(N_2) = \begin{cases} \frac{\frac{1}{K_2(T(N_2))} - \frac{1}{K_2(T(\tilde{N}_2))}}{N_2 - \tilde{N}_2} & , \quad N_2 \neq \tilde{N}_2 \\ - \frac{1}{K_2^2(T(N_2))} \frac{\partial K_2}{\partial T}(T(N_2)) \frac{\partial T}{\partial N_2} \bigg|_{N_2 = \tilde{N}_2} & , \quad N_2 = \tilde{N}_2 \end{cases}$$

(4.5)

Let $r_1(N_2)$, $r_2(U(N_2), N_1)$ and $K_2(T(N_2))$ satisfy the following conditions

$$K_{m2} \leq K_2(T(N_2)) \leq K_{20}, \quad 0 \leq \chi_{12}(N_2) \leq p_{11}, \quad 0 \leq \chi_{21}(N_1, \tilde{N}_2) \leq p_{21},$$

$$0 \leq \chi_{22}(N_1, N_2) \leq p_{22}, \quad 0 \leq \eta_{22}(N_2) \leq k_{22}, \quad i = 1, 2 \quad (4.6)$$

for some positive constants K_{m2} , p_{12} , p_{2i} and k_{22} .

From (4.5), (4.6) and the mean value theorem, we note that

$$|\chi_{12}(N_2)| \leq p_{12}, \quad |\chi_{21}(N_1, \tilde{N}_2)| \leq p_{21}, \quad |\chi_{22}(N_1, N_2)| \leq p_{22} \text{ and}$$

$$|\eta_{22}(N_2)| \leq k_{22}/K_{m2}^2 \quad (4.7)$$

Now $\frac{dV_1}{dt}$ can further be written as

$$\begin{aligned} \frac{dV_1}{dt} \leq & -\frac{r_{10}}{K_1} (N_1 - \tilde{N}_1)^2 + (N_2 - \tilde{N}_2)^2 \left[p_{22} - \frac{r_{20}}{K_2(T(\tilde{N}_2))} \right] \\ & + (N_1 - \tilde{N}_1)(N_2 - \tilde{N}_2) \left[p_{12} + p_{21} \right] \end{aligned} \quad (4.8)$$

Thus $\frac{dV_1}{dt}$ will be negative definite provided

$$p_{22} < \frac{r_{20}}{K_2(T(\tilde{N}_2))} \quad (4.9a)$$

$$\left[p_{12} + p_{21} \right]^2 < 4 \frac{r_{10}}{K_1} \left(\frac{r_{20}}{K_2(T(\tilde{N}_2))} - p_{22} \right) \quad (4.9b)$$

Hence V_1 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium E_8 and hence this equilibrium is globally asymptotically stable provided the conditions (4.9) are satisfied.

5. NUMERICAL EXAMPLE

We provide a numerical example for the model (2.1). The positive equilibrium point i.e. E_4 has been computed and the stability conditions (both local and global) i.e conditions (3.3) and (3.7) are verified and it is found that with the following choice of growth rate and carrying capacity functions and with suitable parameter values, all the conditions are satisfied.

Let us take

$$r_1(N_2) = r_{10} - \frac{a_1 N_2}{1 + r_1 N_2}, \quad K_2(T) = K_{20} - \frac{b_1 T}{1 + m_1 T} \quad \text{and}$$

$$r_2(U, N_1) = r_{20} - \frac{a_2 U}{1 + r_2 U} - \frac{a_3 N_1}{1 + r_3 N_1} \quad (5.1)$$

where $a_1 = 1.0$, $a_2 = 1.0$, $a_3 = 1.0$, $b_1 = 1.0$, $r_1 = 2.2$, $r_2 = 3.2$, $r_3 = 4.1$, $m_1 = 1.02$, $r_{10} = 18.0$, $r_{20} = 20.0$, $K_1 = 6.3859$, $K_{20} = 8.3859$.

Now with this choice of b_1 and m_1 , we have $\frac{b_1 T}{1 + m_1 T} < 1$

Since $K_m \leq K_2(T) \leq K_{20}$, therefore we can choose K_m as $K_m = 6.5$.

We also note from (5.1) that

$$r'_1(N_2) = - \frac{a_1}{(1 + r_1 N_2)^2}, \quad \frac{\partial r_2}{\partial U} = - \frac{a_2}{(1 + r_2 U)^2},$$

$$\frac{\partial r_2}{\partial N_1} = - \frac{a_3}{(1 + r_3 N_1)^2} \quad \text{and} \quad K'_2(T) = - \frac{b_1}{(1 + m_1 T)^2}$$

Therefore ρ_{12} , ρ_{21} , ρ_{22} and k can be chosen as 1.0 each.

Choosing $\alpha = 0.02$, $\delta_0 = 14.0$, $\delta_1 = 15.0$, $\nu = 0.03$, $\theta_0 = 0.02$, $\theta_1 = 0.03$, $\pi = 0.05$, $\lambda = 5.0$, the equilibrium values N_1^* , N_2^* , T^* and U^* are computed as

$$N_2^* = 7.596766, \quad N_1^* = 6.233744, \quad T^* = 2.204474 \quad \text{and} \quad U^* = 0.062529.$$

In table (1), we have computed the equilibrium point E_4 for different values of λ , the rate coefficient of production of toxicant by the first species, and it has been checked that the conditions for local as well global stability of E_4 viz. (3.3a-e)

and (3.7a-e) are satisfied. It has been observed that with increasing λ , N_2^* decreases while there is a slight increment in N_1^* , T^* and U^* increase as expected.

λ	N_2^*	N_1^*	T^*	U^*
3.0	7.717919	6.233609	1.322436	0.037712
3.5	7.680044	6.233651	1.542933	0.043926
4.0	7.648030	6.233686	1.763439	0.050133
4.5	7.620591	6.233717	1.983953	0.056334
5.0	7.596766	6.233744	2.204474	0.062529

Table (1)

6. CONCLUSIONS

In this Chapter, a nonlinear model to study the allelopathic effects between two competing biological species has been proposed and analyzed. One species produces a toxicant in to the environment affecting the other species, living in the same habitat which uptakes this toxicant from the environment. The growth rate and carrying capacity of the affected species are thus decreased caused by uptake and environmental concentrations of the toxicant, respectively. Using stability analysis it has been shown that the equilibrium level of the affected species decreases as the rate of production of the toxicant by the other species increases. It is also noted that if the toxicants are produced continuously in the environment without control, the affected species is doomed to extinction.

CHAPTER - VII

EXISTENCE AND SURVIVAL OF TWO COMPETING SPECIES IN A POLLUTED ENVIRONMENT

1. INTRODUCTION

One of the most important problem that the modern society faces today is pollution of the environment affecting quality of life of people, changing the biodiversity of the habitat, etc. The rapid pace of industrialization is one of the factors, responsible for this change caused by various discharges of hazardous wastes from industries and other human activities, in to both terrestrial and aquatic environments, contaminating air, streams, rivers and oceans with varieties of chemicals and toxic elements. (Grummer, 1961; Nelson, 1970; Patin, 1982; Chattopadhyay, 1996). All these toxic substances adversely affect each and every ecosystem on this planet earth. It is, therefore, essential to study the effects of pollutants/toxicants discharged from various external sources (industrial effluent, vehicular traffic, household wastes, etc.) on the competing biological species living in the polluted environment.

There are various species competing for common resource. Our aim, in this Chapter, is to study that whether it is possible to change the outcome of this competition when the species are affected by toxicants.

The effect of toxicants/pollutants emitted from external sources on biological species have been studied by some

investigators (Hallam et al, 1983a,b; Hallam and De Luna, 1984; De Luna and Hallam, 1987; Freedman and Shukla, 1991; Huaping and Ma, 1991; Shukla and Dubey, 1996). Also some investigators (Hsu and Hubbel, 1979; Goh, 1980; Hsu, 1981a,b; Butler et al, 1983; Freedman, 1987) presented mathematical models for competing species in different situations but without considering the effect of toxicants on the species. In this Chapter, we therefore, propose a non - linear mathematical model, following Freedman and Shukla (1991), to study the effect of a toxicant in a competitive system in a situation where the toxicant is being produced by external sources. It is assumed that each competing species grows logistically and its growth rate is affected by the presence of the other competitor. It is also assumed that the growth rate of the competitor decreases as the uptake concentration, which is different for each competitor (see Huaping and Ma, 1991), of toxicant increases but its carrying capacity decreases due to the presence of toxicant in the environment. It is further assumed that the toxicant is being produced in the environment by some external sources and is depleted by some natural degradation factors. It is considered that the growth rate of uptake concentration of toxicant by each competitor is proportional to the density of this competitor and the environmental concentration of the toxicant and the increase in the growth rate of uptake concentration of the toxicant is same as the corresponding decrease in the environmental concentration of the toxicant. The stability theory of differential equation (La Salle and Lefschetz, 1961; Freedman, 1987) is used to analyze the model.

We assume that all functions utilized here are sufficiently smooth and that the solutions to the initial value problem exists uniquely and are continuous for all positive values of time.

2. MATHEMATICAL MODEL

We consider a closed polluted environment where two species are competing and are affected by the same toxicant being emitted in to the environment by some external source. We assume that both the competitors have different uptake concentrations of toxicant. Using the similar arguments as Freedman and Shukla (1991), the system is assumed to be governed by following non linear differential equations :

$$\begin{aligned}\frac{dN_1}{dt} &= r_1(U_1)N_1 - \frac{r_{10}N_1^2}{K_1(T)} - \beta_1N_1N_2 \\ \frac{dN_2}{dt} &= r_2(U_2)N_2 - \frac{r_{20}N_2^2}{K_2(T)} - \beta_2N_1N_2 \\ \frac{dT}{dt} &= Q(t) - \delta_0T - \alpha_1N_1T - \alpha_2N_2T + \pi_1\nu_1N_1U_1 + \pi_2\nu_2N_2U_2 \\ \frac{dU_1}{dt} &= -\delta_1U_1 + \alpha_1N_1T - \nu_1N_1U_1 \\ \frac{dU_2}{dt} &= -\delta_2U_2 + \alpha_2N_2T - \nu_2N_2U_2\end{aligned}\tag{2.1}$$

$$\begin{aligned}N_1(0) &= N_{10} \geq 0, N_2(0) = N_{20} \geq 0, T(0) = T_0 \geq 0, U_1(0) = c_1N_{10}, \\ U_2(0) &= c_2N_{20}, c_1 > 0, c_2 > 0, 0 \leq \pi_1 \leq 1, 0 \leq \pi_2 \leq 1.\end{aligned}$$

Here $N_i(t)$ ($i = 1, 2$) is the density of the i -th competitor, $Q(t)$ is the rate of emission of toxicant by some external source

like chimney or vehicular traffic with the concentration $T(t)$ into the environment which is assumed to be either instantaneous ($Q(t) = 0$) or a constant say Q_0 , $U_i(t)$ is the uptake concentration of toxicant by the i -th competitor, $\delta_0 > 0$ is the natural washout rate coefficient of $T(t)$, $\alpha_i > 0$ is the depletion rate coefficient of $T(t)$ due to its uptake by the i -th competitor, $\delta_i > 0$ is the natural washout rate coefficient of $U_i(t)$, $\nu_i > 0$ is the depletion rate coefficient of $U_i(t)$ due to decay of some members of $N_i(t)$ and a fraction π_i of which may reenter into the environment, $c_i \geq 0$ is the proportionality constant determining the measure of initial toxicant concentration in the i -th competitor at $t = 0$. It is assumed in modelling the system (2.1) that the growth rate of uptake concentration $U_i(t)$ increases with $\alpha_i N_i T$ which denotes the rate of depletion of the toxicant in the environment due to its uptake by the i -th competitor. The competition coefficients β_1 and β_2 are assumed to be positive in the model.

In our model (2.1), the function $r_i(U_i)$ denotes the growth rate coefficient of i -th competitor which decreases with U_i and hence we assume that

$$r_i(0) = r_{i0} > 0, \quad \frac{dr_i}{dU_i} < 0 \quad \text{for } U_i > 0 \quad (2.2a)$$

where $i = 1, 2$.

Similarly, the function $K_i(T)$ denotes the maximum population density of the i -th competitor which the environment can support and it also decreases with T and hence we assume that

$$K_i(0,0) = K_{i0} > 0, \quad \frac{dK_i}{dT} < 0 \quad \text{for } T > 0 \quad (2.2b)$$

where $i = 1, 2$.

3. MATHEMATICAL ANALYSIS

3.1. CASE I: WHEN THE EMISSION OF THE TOXICANT IS INSTANTANEOUS, i.e. $Q(t) = 0$

In this case, at $t = 0$, the toxicant is discharged in to the environment at concentration T_0 . Since $Q(t) = 0$, the model (2.1) has four nonnegative equilibria, namely $E_1(0,0,0,0,0)$, $E_2(K_{10},0,0,0,0)$, $E_3(0,K_{20},0,0,0)$ and $E_4(N_1^0, N_2^0, 0,0,0)$.

Here N_1^0 and N_2^0 are given by

$$\begin{aligned} N_1^0 &= \frac{r_{20}K_{10}(\beta_1 K_{20} - r_{10})}{\beta_1 \beta_2 K_{10} K_{20} - r_{10} r_{20}} \\ N_2^0 &= \frac{r_{10}K_{20}(\beta_2 K_{10} - r_{20})}{\beta_1 \beta_2 K_{10} K_{20} - r_{10} r_{20}} \end{aligned} \quad (3.1)$$

Thus for the existence of E_4 , we must have the following two cases :

$$\text{Case (i)} \quad \frac{r_{10}}{\beta_1} > K_{20} , \quad \frac{r_{20}}{\beta_2} > K_{10}$$

$$\text{Case (ii)} \quad \frac{r_{10}}{\beta_1} < K_{20} , \quad \frac{r_{20}}{\beta_2} < K_{10}$$

STABILITY ANALYSIS:

Let M_i be the variational matrices corresponding to E_i , $i = 1, 2, 3, 4$. Then we have

$$M_1 = \begin{bmatrix} r_{10} & 0 & 0 & 0 & 0 \\ 0 & r_{20} & 0 & 0 & 0 \\ 0 & 0 & -\delta_0 & 0 & 0 \\ 0 & 0 & 0 & -\delta_1 & 0 \\ 0 & 0 & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -r_{10} & -\beta_1 K_{10} & r_{10} K'_1(0) & r'_1(0) K_{10} & 0 \\ 0 & r_{20} - \beta_2 K_{10} & 0 & 0 & 0 \\ 0 & 0 & -(\delta_0 + \alpha_1 K_{10}) & \pi_1 \nu_1 K_{10} & 0 \\ 0 & 0 & \alpha_1 K_{10} & -(\delta_1 + \nu_1 K_{10}) & 0 \\ 0 & 0 & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$M_3 = \begin{bmatrix} r_{10} - \beta_1 K_{20} & 0 & 0 & 0 & 0 \\ -\beta_2 K_{20} & -r_{20} & r_{20} K'_2(0) & 0 & r'_2(0) K_{20} \\ 0 & 0 & -(\delta_0 + \alpha_2 K_{20}) & 0 & \pi_2 \nu_2 K_{20} \\ 0 & 0 & 0 & -\delta_1 & 0 \\ 0 & 0 & \alpha_2 K_{20} & 0 & -(\delta_2 + \nu_2 K_{20}) \end{bmatrix}$$

$$M_4 = \begin{bmatrix} -\frac{r_{10}}{K_{10}} N_1^0 & -\beta_1 N_1^0 & \frac{r_{10}}{K_{10}^2} K'_1(0) N_1^{0^2} & r'_1(0) N_1^0 & 0 \\ -\beta_2 N_2^0 & -\frac{r_{20}}{K_{20}} N_2^0 & \frac{r_{20}}{K_{20}^2} K'_2(0) N_2^{0^2} & 0 & r'_2(0) N_2^0 \\ 0 & 0 & -(\delta_0 + \alpha_1 N_1^0 + \alpha_2 N_2^0) & \pi_1 \nu_1 N_1^0 & \pi_2 \nu_2 N_2^0 \\ 0 & 0 & \alpha_1 N_1^0 & -(\delta_1 + \nu_1 N_1^0) & 0 \\ 0 & 0 & \alpha_2 N_2^0 & 0 & -(\delta_1 + \nu_1 N_1^0) \end{bmatrix}$$

From M_1 , we note that E_1 is a hyperbolic saddle point whose unstable manifold is locally N_1 - N_2 space and whose stable manifold is locally in T - U_1 - U_2 space. From M_2 , we see that E_2 is locally

asymptotically stable provided $\frac{r_{20}}{\beta_2} < K_{10}$. Similarly, from M_3 , we see that E_3 is locally asymptotically stable provided $\frac{r_{10}}{\beta_1} < K_{20}$.

From M_4 we see that E_4 is locally asymptotically stable iff

$$\frac{r_{10}}{K_{10}} N_1^0 - \frac{r_{20}}{K_{20}} N_2^0 > \beta_1 N_1^0 \beta_2 N_2^0 \quad \text{i.e.} \quad \frac{r_{10}}{K_{10}} \frac{r_{20}}{K_{20}} > \beta_1 \beta_2 \quad (3.2)$$

Thus, we note that under the case (i), i.e.

$\frac{r_{10}}{\beta_1} > K_{20}$, $\frac{r_{20}}{\beta_2} > K_{10}$, E_2 and E_3 are unstable (rather they are saddle points) and E_4 is locally asymptotically stable, as the condition (3.2) is satisfied. However, in case (ii) i.e.

$\frac{r_{10}}{\beta_1} < K_{20}$, $\frac{r_{20}}{\beta_2} < K_{10}$, E_2 and E_3 are locally asymptotically stable and E_4 is unstable.

In the following theorem we state that E_4 is globally asymptotically stable under case (i).

.

THEOREM 3.1 If $N_1(0) > 0$ and $N_2(0) > 0$, then E_4 is globally asymptotically stable.

This theorem can be proved on similar lines as the proof of Theorem (3.3) by taking $Q_0 = 0$ correspondingly.

3.2. CASE II: WHEN THE EMISSION RATE OF THE TOXICANT IS A CONSTANT

$$\text{i.e. } Q(t) = Q_0$$

In this case, the model (2.1) has four nonnegative equilibria, namely $\bar{E}_1(0, 0, \frac{Q_0}{\delta_0}, 0, 0)$, $\bar{E}_2(\tilde{N}_1, 0, \tilde{T}, \tilde{U}_1, 0)$, $\bar{E}_3(0, \hat{N}_2, \hat{T}, 0, \hat{U}_2)$ and $\bar{E}_4(N_1^*, N_2^*, T^*, U_1^*, U_2^*)$. The existence of \bar{E}_1 is obvious. We shall show the existence of \bar{E}_2 , \bar{E}_3 and \bar{E}_4 as follows.

EXISTENCE OF \bar{E}_2 :

Here \tilde{N}_1 , \tilde{T} and \tilde{U}_1 are the positive solution of the system of equations

$$N_1 = r_1(U_1) K_1(T)/r_{10} \quad (3.3a)$$

$$T = \frac{Q_0(\delta_1 + \nu_1 N_1)}{f_1(N_1)} = h_1(N_1) \quad (\text{say}) \quad (3.3b)$$

$$U_1 = \frac{Q_0 \alpha_1 N_1}{f_1(N_1)} = g_1(N_1) \quad (\text{say}) \quad (3.3c)$$

$$\text{where } f_1(N_1) = \delta_0 \delta_1 + (\delta_0 \nu_1 + \alpha_1 \delta_1) N_1 + \alpha_1 \nu_1 (1 - \pi_1) N_1^2 \quad (3.3d)$$

We note that T and U_1 increase as Q_0 increases. Thus $r_1(U_1)$ and $K_1(T)$ decrease as Q_0 increases making \tilde{N}_1 to decrease with increasing Q_0 . (see equation (3.4a)).

Letting $F(N_1) = r_{10} N_1 - r_1(g_1(N_1)) K_1(h_1(N_1)) = 0 \quad (3.4a)$,
we note that

$$F(0) < 0 \text{ and } F(K_{10}) > 0.$$

This guarantees the existence of a root of $F(N_1) = 0$ for $0 < N_1 < K_{10}$, say \tilde{N}_1 . Further, this root will be unique provided

$$F'(N_1) = r_{10} - \left\{ r_1 \frac{dK_1}{dT} \frac{dh_1}{dN_1} + K_1 \frac{dr_1}{dU_1} \frac{dg_1}{dN_1} \right\} > 0 \quad (3.4b)$$

Knowing the value of \tilde{N}_1 , the values of \tilde{T} and \tilde{U}_1 can be computed from equations (3.4b) and (3.4c).

EXISTENCE OF \bar{E}_3 :

In this case, \hat{N}_2 , \hat{T} and \hat{U}_2 are the positive solution of the system of equations

$$N_2 = r_2(U_2) K_2(T)/r_{20} \quad (3.5a)$$

$$T = \frac{Q_0(\delta_2 + \nu_2 N_2)}{f_2(N_2)} = h_2(N_2) \quad (\text{say}) \quad (3.5b)$$

$$U_2 = \frac{Q_0 \alpha_2 N_2}{f_2(N_2)} = g_2(N_2) \quad (\text{say}) \quad (3.5c)$$

$$\text{where } f_2(N_2) = \delta_0 \delta_2 + (\delta_0 \nu_2 + \alpha_2 \delta_2) N_2 + \alpha_2 \nu_2 (1 - \pi_2) N_2^2 \quad (3.5d)$$

We note that T and U_2 increase as Q_0 increases. Thus $r_2(U_2)$ and $K_2(T)$ decrease as Q_0 increases making \hat{N}_2 to decrease with increasing Q_0 . (see equation (3.5e)).

$$\text{Letting } G(N_2) = r_{20} N_2 - r_2(g_2(N_2)) K_2(h_2(N_2)) = 0 \quad (3.5e),$$

we note that

$$G(0) < 0 \text{ and } G(K_{20}) > 0.$$

This guarantees the existence of a root of $G(N_2) = 0$ for $0 < N_2 < K_{20}$, say \hat{N}_2 . Further, this root will be unique provided

$$G'(N_2) = r_{20} - \left\{ r_2 \frac{dK_2}{dT} \frac{dh_2}{dN_2} + K_2 \frac{dr_2}{dU_2} \frac{dg_2}{dN_2} \right\} > 0 \quad (3.5f)$$

Knowing the value of \hat{N}_2 , the values of \hat{T} and \hat{U}_2 can be computed from equations (3.5b) and (3.5c).

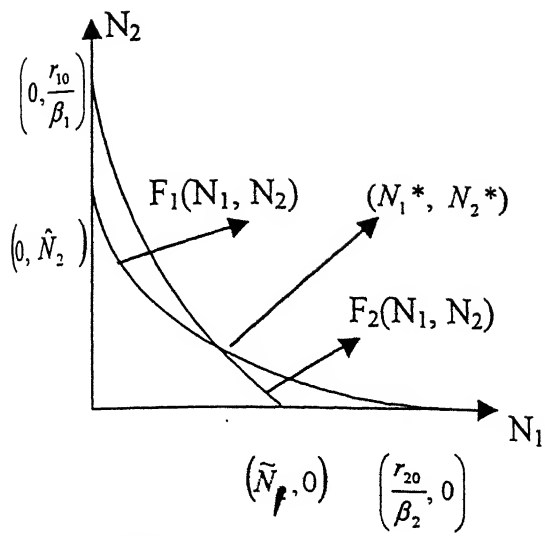
EXISTENCE OF \bar{E}_4 :

Here

$$\beta_1 N_2 = r_1(U_1) - r_{10} \frac{N_1}{K_1(T)} \quad (3.6a)$$

$$\beta_2 N_1 = r_2(U_2) - r_{20} \frac{N_2}{K_2(T)} \quad (3.6b)$$

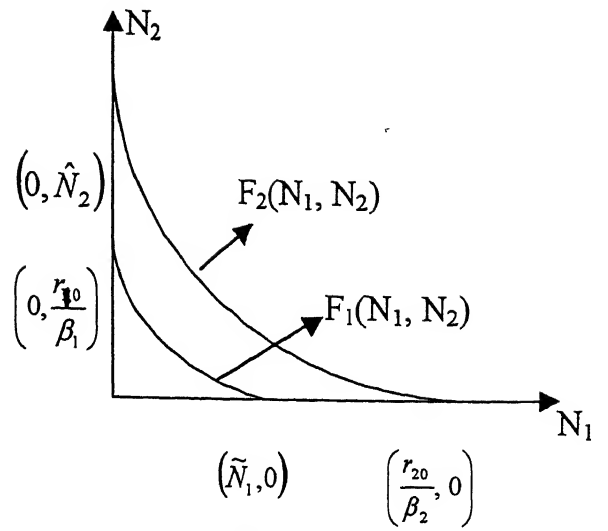
$$T = \frac{Q_0(\delta_1 + \nu_1 N_1)(\delta_2 + \nu_2 N_2)}{f(N_2)(\delta_1 + \nu_1 N_1) + f_1(N_1)(\delta_2 + \nu_2 N_2)} = h(N_1, N_2) \quad (3.6c)$$



Case when

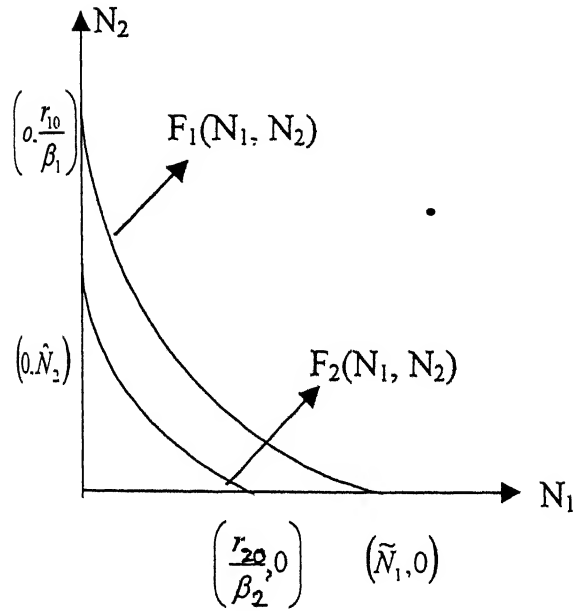
$$\tilde{N}_1 < \frac{r_{20}}{\beta_2} \quad , \quad \hat{N}_2 < \frac{r_{10}}{\beta_1}$$

Case (i)



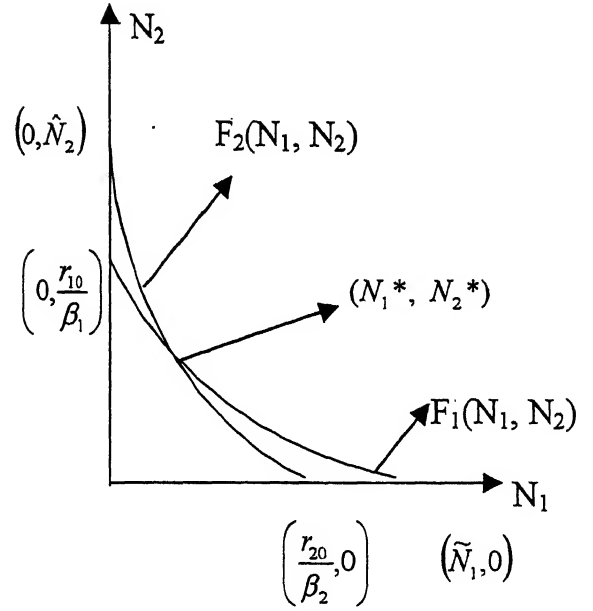
Case when

$$\tilde{N}_1 < \frac{r_{20}}{\beta_2} \quad , \quad \hat{N}_2 > \frac{r_{10}}{\beta_1}$$



Case when

$$\tilde{N}_1 > \frac{r_{20}}{\beta_2} \quad , \quad \hat{N}_2 < \frac{r_{10}}{\beta_1}$$



Case when

$$\tilde{N}_1 > \frac{r_{20}}{\beta_2} \quad , \quad \hat{N}_2 > \frac{r_{10}}{\beta_1}$$

Case (ii)

Fig (1)

This point of intersection will give N_1^*, N_2^* . For uniqueness of (N_1^*, N_2^*) , we must have $\frac{dN_2}{dN_1} < 0$ for both the curves in R.

For the curve (I),

$$\frac{dN_2}{dN_1} = \frac{r_{10} - K_1(h) \frac{dr_1}{dU_1} \frac{\partial g_{12}}{\partial N_1} - \left(r_1(g_{12}) - \beta_1 N_2 \right) \frac{dK_1}{dT} \frac{\partial h}{\partial N_1}}{K_1(h) \left(\frac{dr_1}{dU_1} \frac{\partial g_{12}}{\partial N_2} - \beta_1 \right) + \left(r_1(g_{12}) - \beta_1 N_2 \right) \frac{dK_1}{dT} \frac{\partial h}{\partial N_2}} \quad (3.9a)$$

and for the curve (II),

$$\frac{dN_2}{dN_1} = \frac{K_2(h) \left(\frac{dr_2}{dU_2} \frac{\partial g_{21}}{\partial N_1} - \beta_2 \right) + \left(r_2(g_{21}) - \beta_2 N_1 \right) \frac{dK_2}{dT} \frac{\partial h}{\partial N_1}}{r_{20} - K_2(h) \frac{dr_2}{dU_2} \frac{\partial g_{21}}{\partial N_2} - \left(r_2(g_{21}) - \beta_2 N_1 \right) \frac{dK_2}{dT} \frac{\partial h}{\partial N_2}} \quad (3.9b)$$

In case (i), the absolute value of $\frac{dN_2}{dN_1}$ given by (3.9a) is less than the absolute value of $\frac{dN_2}{dN_1}$ given by (3.9b). For the case (ii), just the opposite is the condition.

Knowing the values of N_1^*, N_2^* ; T^*, U_1^* and U_2^* can be computed from equations (3.6c) - (3.6e).

STABILITY ANALYSIS

To study the local stability behavior of the equilibria, we compute the variational matrices corresponding to these equilibria. Now using the analogous notations for the variational matrices we have,

$$\bar{M}_1 = \begin{bmatrix} r_{10} & 0 & 0 & 0 & 0 \\ 0 & r_{20} & 0 & 0 & 0 \\ -\frac{\alpha_1 Q_0}{\delta_0} & -\frac{\alpha_2 Q_0}{\delta_0} & -\delta_0 & 0 & 0 \\ \frac{\alpha_1 Q_0}{\delta_0} & 0 & 0 & -\delta_1 & 0 \\ 0 & \frac{\alpha_2 Q_0}{\delta_0} & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$\bar{M}_2 = \begin{bmatrix} -r_1(\tilde{U}_1) & -\beta_1 \tilde{N}_1 & G_{11} & r'_1(\tilde{U}_1) \tilde{N}_1 & 0 \\ 0 & r_{20} - \beta_2 \tilde{N}_1 & 0 & 0 & 0 \\ -(\alpha_1 \tilde{T} - \pi_1 \nu_1 \tilde{U}_1) & -\alpha_2 \tilde{T} & -(\delta_0 + \alpha_1 \tilde{N}_1) & \pi_1 \nu_1 \tilde{N}_1 & 0 \\ \alpha_1 \tilde{T} - \nu_1 \tilde{U}_1 & 0 & \alpha_1 \tilde{N}_1 & -(\delta_1 + \nu_1 \tilde{N}_1) & 0 \\ 0 & \alpha_2 \tilde{T} & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$\bar{M}_3 = \begin{bmatrix} r_{10} - \beta_1 \hat{N}_2 & 0 & 0 & 0 & 0 \\ -\beta_2 \hat{N}_2 & -r_2(\hat{U}_2) & G_{12} & 0 & r'_2(\hat{U}_2) \hat{N}_2 \\ -\alpha_1 \hat{T} & -(\alpha_2 \hat{T} - \pi_2 \nu_2 \hat{U}_2) & -(\delta_0 + \alpha_2 \hat{N}_2) & 0 & \pi_2 \nu_2 \hat{N}_2 \\ \alpha_1 \hat{T} & 0 & 0 & -\delta_1 & 0 \\ 0 & (\alpha_2 \hat{T} - \pi_2 \nu_2 \hat{U}_2) & \alpha_2 \hat{N}_2 & 0 & -(\delta_2 + \nu_2 \hat{N}_2) \end{bmatrix}$$

$$\bar{M}_4 = \begin{bmatrix} -\frac{r_{10}N_1^*}{K_1(T^*)} - \beta_1 N_1^* & G_{21} & r'_1(U_1^*)N_1^* & 0 \\ -\beta_2 N_2^* - \frac{r_{20}N_2^*}{K_2(T^*)} & G_{22} & 0 & r'_2(U_2^*)N_2^* \\ G_{31} & G_{32} & -(\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) & \pi_1 \nu_1 N_1^* & \pi_2 \nu_2 N_2^* \\ G_{41} & 0 & \alpha_1 N_1^* & -(\delta_1 + \nu_1 N_1^*) & 0 \\ 0 & G_{42} & \alpha_2 N_2^* & 0 & -(\delta_2 + \nu_2 N_2^*) \end{bmatrix}$$

Where

$$\begin{aligned} G_{11} &= \frac{r_1^2(\tilde{U}_1)}{r_{10}} K'_1(\tilde{T}) , & G_{12} &= \frac{r_2^2(\hat{U}_2)}{r_{20}} K'_2(\hat{T}) , \\ G_{21} &= \frac{r_{10}N_1^{*2}}{K_1^2(T^*)} K'_1(T^*) , & G_{22} &= \frac{r_{20}N_2^{*2}}{K_2^2(T^*)} K'_2(T^*) , \\ G_{31} &= -(\alpha_1 T^* - \pi_1 \nu_1 U_1^*) , & G_{32} &= -(\alpha_2 T^* - \pi_2 \nu_2 U_2^*) , \\ G_{41} &= \alpha_1 T^* - \nu_1 U_1^* , & G_{42} &= \alpha_2 T^* - \nu_2 U_2^* \end{aligned} \quad (3.10)$$

From \bar{M}_1 we note that \bar{E}_1 is a saddle point with unstable manifold locally in N_1 - N_2 space and unstable manifold locally in T - U_1 - U_2 space.

From \bar{M}_2 we note that \bar{E}_2 is locally asymptotically stable provided

$$\tilde{N}_1 > \frac{r_{20}}{\beta_2} \quad (3.11a)$$

$$\text{and} \quad \delta_0 + \alpha_1 \tilde{N}_1 > \left(\frac{-K'_1(\tilde{T})}{K_1(\tilde{T})} \right) \left(Q_0 - \delta_0 \tilde{T} \right) \quad (3.11b)$$

otherwise, it is unstable.

From \bar{M}_3 we note that \bar{E}_3 is locally asymptotically stable provided

$$\tilde{N}_2 > \frac{r_{10}}{\beta_1} \quad (3.12a)$$

and
$$\delta_0 + \alpha_2 \hat{N}_2 > \left[\frac{-K'_2(\hat{T})}{K_2(\hat{T})} \right] \left(Q_0 - \delta_0 \hat{T} \right) \quad (3.12b)$$

otherwise, it is unstable.

From \bar{M}_4 , it is not obvious to know the behavior of \bar{E}_4 . We, therefore use Lyapunov's stability theorem to study its behavior.

In the following theorem we are able to find certain conditions under which \bar{E}_4 is locally asymptotically stable.

THEOREM 3.2 Let the following inequalities hold:

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \quad (3.13a)$$

$$\left[-\frac{r_{10}N_1^*}{K_1^2(T^*)} K'_1(T^*) + \left(\alpha_1 T^* - \pi_1 \nu_1 U_1^* \right) \right]^2 < \frac{1}{3} \frac{r_{10}}{K_1(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.13b)$$

$$\left[r'_1(U_1^*) + \left(\alpha_1 T^* - \nu_1 U_1^* \right) \right]^2 < \frac{2}{3} \frac{r_{10}}{K_1(T^*)} (\delta_1 + \nu_1 N_1^*) \quad (3.13c)$$

$$\left[-\frac{\beta_1}{\beta_2} \frac{r_{20}N_2^*}{K_2^2(T^*)} K'_2(T^*) + \left(\alpha_2 T^* - \pi_2 \nu_2 U_2^* \right) \right]^2 < \frac{1}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.13d)$$

$$\left[\frac{\beta_1}{\beta_2} r'_2(U_2^*) + \left(\alpha_2 T^* - \nu_2 U_2^* \right) \right]^2 < \frac{2}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_2 + \nu_2 N_2^*) \quad (3.13e)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_1 + \nu_1 N_1^*) \quad (3.13f)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_2 + \nu_2 N_2^*) \quad (3.13g)$$

Then \bar{E}_4 is locally asymptotically stable under the case (i).

PROOF: In order to prove the local asymptotic stability of \bar{E}_4 , let us take the following perturbations around the equilibrium \bar{E}_4 :

$$N_1 = N_1^* + n_1, \quad N_2 = N_2^* + n_2, \quad T = T^* + \tau, \quad U_1 = U_1^* + u_1, \quad U_2 = U_2^* + u_2$$

where n_1, n_2, τ, u_1, u_2 are small perturbations from \bar{E}_4 .

Then the linearized system of (2.1)

$$\dot{n}_1 = - \frac{r_{10}N_1^*}{K_1(T^*)} n_1 - \beta_1 N_1^* n_2 + \frac{r_{10}N_1^*}{K_1^2(T^*)} K_1'(T^*) \tau + r_1'(U_1^*) N_1^* u_1$$

$$\dot{n}_2 = - \beta_2 N_2^* n_1 - \frac{r_{20}N_2^*}{K_2(T^*)} n_2 + \frac{r_{20}N_2^*}{K_2^2(T^*)} K_2'(T^*) \tau + r_2'(U_2^*) N_2^* u_2$$

$$\begin{aligned} \dot{\tau} = & - (\alpha_1 T^* - \pi_1 \nu_1 U_1^*) n_1 - (\alpha_2 T^* - \pi_2 \nu_2 U_2^*) n_2 - (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \tau \\ & + \pi_1 \nu_1 N_1^* u_1 + \pi_2 \nu_2 N_2^* u_2 \end{aligned}$$

$$\dot{u}_1 = (\alpha_1 T^* - \nu_1 U_1^*) n_1 + \alpha_1 N_1^* \tau - (\delta_1 + \nu_1 N_1^*) u_1$$

$$\dot{u}_2 = (\alpha_2 T^* - \nu_2 U_2^*) n_2 + \alpha_2 N_2^* \tau - (\delta_2 + \nu_2 N_2^*) u_2 \quad (3.14)$$

Now consider the following positive definite function

$$V = \frac{1}{2} r_1^2 + \frac{1}{2} b_1 n_2^2 + \frac{1}{2} \tau^2 + \frac{1}{2} u_1^2 + \frac{1}{2} u_2^2 \quad (3.15)$$

$$\text{Then } \dot{V} = n_1 \dot{n}_1 + b_1 n_2 \dot{n}_2 + \tau \dot{\tau} + u_1 \dot{u}_1 + u_2 \dot{u}_2$$

substituting values of $\dot{n}_1, \dot{n}_2, \dot{\tau}, \dot{u}_1$ and \dot{u}_2 from (3.14) in to this equation and with a little algebraic manipulation, we get

$$\begin{aligned}
\dot{V} = & -\frac{1}{2} a_{11} n_1^2 + a_{12} n_1 n_2 - \frac{1}{2} a_{22} n_2^2 \\
& -\frac{1}{2} a_{11} n_1^2 + a_{13} n_1 \tau - \frac{1}{2} a_{33} \tau^2 \\
& -\frac{1}{2} a_{11} n_1^2 + a_{14} n_1 u_1 - \frac{1}{2} a_{44} u_1^2 \\
& -\frac{1}{2} a_{22} n_2^2 + a_{23} n_2 \tau - \frac{1}{2} a_{33} \tau^2 \\
& -\frac{1}{2} a_{22} n_2^2 + a_{25} n_2 u_2 - \frac{1}{2} a_{55} u_2^2 \\
& -\frac{1}{2} a_{33} \tau^2 + a_{34} \tau u_1 - \frac{1}{2} a_{44} u_1^2 \\
& -\frac{1}{2} a_{33} \tau^2 + a_{35} \tau u_2 - \frac{1}{2} a_{55} u_2^2
\end{aligned} \tag{3.16}$$

$$\text{where } a_{11} = \frac{2}{3} \frac{r_{10}}{K_1(T^*)}, \quad a_{22} = \frac{2}{3} b_1 \frac{r_{20}}{K_2(T^*)},$$

$$a_{33} = \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*), \quad a_{44} = (\delta_1 + \nu_1 N_1^*), \quad a_{55} = (\delta_2 + \nu_2 N_2^*),$$

$$a_{12} = \beta_1 + b_1 \beta_2, \quad a_{13} = -\frac{r_{10} N_1^*}{K_1^2(T^*)} K_1'(T^*) + \left(\alpha_1 T^* - \pi_1 \nu_1 U_1^* \right),$$

$$a_{14} = r_1'(U_1^*) + \left(\alpha_1 T^* - \nu_1 U_1^* \right), \quad a_{25} = b_1 r_2'(U_2^*) + \left(\alpha_2 T^* - \nu_2 U_2^* \right),$$

$$a_{23} = -b_1 \frac{r_{20} N_2^*}{K_2^2(T^*)} K_2'(T^*) + \left(\alpha_2 T^* - \pi_2 \nu_2 U_2^* \right),$$

$$a_{34} = (\pi_1 \nu_1 + \alpha_1) N_1^*, \quad a_{35} = (\pi_2 \nu_2 + \alpha_2) N_2^* \tag{3.17}$$

From (3.16) and (3.17) we note that \dot{V} will be negative definite provided

$$\begin{aligned}
a_{12}^2 & < a_{11} a_{22}, \quad a_{13}^2 < a_{11} a_{33}, \quad a_{14}^2 < a_{11} a_{44}, \quad a_{23}^2 < a_{22} a_{33}, \\
a_{25}^2 & < a_{22} a_{55}, \quad a_{34}^2 < a_{33} a_{44}, \quad a_{35}^2 < a_{33} a_{55}.
\end{aligned} \tag{3.18}$$

The first condition i.e. $a_{12}^2 < a_{11} a_{22}$ gives

$$\left[\beta_1 + b_1 \beta_2 \right]^2 < \frac{4}{9} b_1 \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)}$$

by choosing $b_1 = \frac{\beta_1}{\beta_2}$ which reduces to

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \text{ which is (3.13a).}$$

The rest of the conditions (3.18) respectively imply the conditions (3.13b-g).

This shows that under the conditions (3.13) \dot{V} is negative definite showing that V is a Lyapunov's function for the linearized system and hence the proof of the theorem (3.1) follows.

In the following theorem we show that \bar{E}_4 is globally asymptotically stable. To prove this theorem we first need the following lemma which we state without proof. This lemma establishes a region of attraction for our system (2.1).

LEMMA 3.1 The set

$\Omega_1 = \left\{ (N_1, N_2, T, U_1, U_2) : 0 \leq N_1 \leq K_{10}, 0 \leq N_2 \leq K_{20}, \right.$
 $\left. 0 \leq T + U_1 + U_2 \leq Q_0/\delta, \delta = \min(\delta_0, \delta_1, \delta_2) \right\}$ attracts all solutions initiating in the positive orthant.

THEOREM 3.3 In addition to the assumptions (2.2) and (2.3), let $r_i(U_i)$ and $K_i(T)$ satisfy in Ω_1 :

$$K_{mi} \leq K(T) \leq K_{i0}, 0 \leq -r'_i(U_i) \leq p_i, 0 \leq -K'_i(T) \leq q_i$$

for $i = 1, 2$ (3.19)

for some positive constants K_{mi} , p_i and q_i .

Then if the following inequalities hold :

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \quad (3.20a)$$

$$\left[\frac{r_{10} q_1 K_{10}}{K_{m1}^2} + (\alpha_1 + \pi_1 \nu_1) \frac{Q_0}{\delta} \right]^2 < \frac{1}{3} \frac{r_{10}}{K_1(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.20b)$$

$$\left[p_1 + (\alpha_1 + \nu_1) \frac{Q_0}{\delta} \right]^2 < \frac{2}{3} \frac{r_{10}}{K_1(T^*)} (\delta_1 + \nu_1 N_1^*) \quad (3.20c)$$

$$\left[\frac{\beta_1}{\beta_2} \frac{r_{20} q_2 K_{20}}{K_{m2}^2} + (\alpha_2 + \pi_2 \nu_2) \frac{Q_0}{\delta} \right]^2 < \frac{1}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.20d)$$

$$\left[\frac{\beta_1}{\beta_2} p_2 + (\alpha_2 + \nu_2) \frac{Q_0}{\delta} \right]^2 < \frac{2}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_2 + \nu_2 N_2^*) \quad (3.20e)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_1 + \nu_1 N_1^*) \quad (3.20f)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_2 + \nu_2 N_2^*) \quad (3.20g)$$

\bar{E}_4 is globally asymptotically stable in Ω_1 under case (i).

PROOF: We consider the following positive definite function about

\bar{E}_4 ,

$$\begin{aligned} W(N_1, N_1, T, U_1, U_1) &= \left(N_1 - N_1^* - N_1^* \ln \frac{N_1}{N_1^*} \right) \\ &+ b_2 \left(N_2 - N_2^* - N_2^* \ln \frac{N_2}{N_2^*} \right) + \frac{1}{2} (T - T^*)^2 \\ &+ \frac{1}{2} (U_1 - U_1^*)^2 + \frac{1}{2} (U_2 - U_2^*)^2 \end{aligned} \quad (3.21)$$

Differentiating W with respect to t along the solution of (2.1), we get

$$\begin{aligned}
\dot{W} = & (N_1 - N_1^*) \left[r_1(U_1) - \frac{r_{10}N_1}{K_1(T)} - \beta_1 N_2 \right] \\
& + b_2 (N_2 - N_2^*) \left[r_2(U_2) - \frac{r_{20}N_2}{K_2(T)} - \beta_2 N_1 \right] \\
& + (T - T^*) \left[Q_0 - \delta_0 T - \alpha_1 N_1 T - \alpha_2 N_2 T + \pi_1 \nu_1 N_1 U_1 + \pi_2 \nu_2 N_2 U_2 \right] \\
& + (U_1 - U_1^*) \left[-\delta_1 U_1 + \alpha_1 N_1 T - \nu_1 N_1 U_1 \right] \\
& + (U_2 - U_2^*) \left[-\delta_2 U_2 + \alpha_2 N_2 T - \nu_2 N_2 U_2 \right] \tag{3.22}
\end{aligned}$$

Using (3.6), a little algebraic manipulation yields,

$$\begin{aligned}
\dot{W} = & - \frac{r_{10}}{K_1(T^*)} (N_1 - N_1^*)^2 - b_2 \frac{r_{20}}{K_2(T^*)} (N_2 - N_2^*)^2 \\
& - (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (T - T^*)^2 - (\delta_1 + \nu_1 N_1^*) (U_1 - U_1^*)^2 \\
& - (\delta_2 + \nu_2 N_2^*) (U_2 - U_2^*)^2 \\
& + (N_1 - N_1^*) (N_2 - N_2^*) \left[\beta_1 + b_2 \beta_2 \right] \\
& + (N_1 - N_1^*) (T - T^*) \left[-r_{10} \eta_1(T) N_1 - (\alpha_1 T - \pi_1 \nu_1 U_1) \right] \\
& + (N_1 - N_1^*) (U_1 - U_1^*) \left[\xi_1(U_1) + (\alpha_1 T - \nu_1 U_1) \right] \\
& + (N_2 - N_2^*) (T - T^*) \left[-b_2 r_{20} \eta_2(T) N_2 - (\alpha_2 T - \pi_2 \nu_2 U_2) \right] \\
& + (N_2 - N_2^*) (U_2 - U_2^*) \left[b_2 \xi_2(U_2) + (\alpha_2 T - \nu_2 U_2) \right] \\
& + (T - T^*) (U_1 - U_1^*) \left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right] \\
& + (T - T^*) (U_2 - U_2^*) \left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right] \tag{3.23}
\end{aligned}$$

where

$$\xi_i(U_i) = \begin{cases} \frac{r_i(U_i) - r_i(U_i^*)}{(U_i - U_i^*)} & , \quad U_i \neq U_i^* \\ r_i'(U_i^*) & , \quad U_i = U_i^* \end{cases}$$

$$\eta_i(T) = \begin{cases} \left[\frac{1}{K_i(T)} - \frac{1}{K_i(T^*)} \right] / (T - T^*), & T \neq T^* \\ - \frac{K'_i(T^*)}{K_i^2(T^*)}, & T = T^* \end{cases}, \quad (3.24)$$

Using (3.24) and mean value theorem, we get

$$|\xi_i(U_i)| \leq p_i, \quad |\eta_i(T)| \leq q_i/K_{mi}^2 \quad \text{for } i = 1, 2. \quad (3.25)$$

\dot{W} can further be written as sum of the quadratics,

$$\begin{aligned} \dot{W} = & -\frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{12} (N_1 - N_1^*) (N_2 - N_2^*) - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 \\ & - \frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{13} (N_1 - N_1^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{14} (N_1 - N_1^*) (U_1 - U_1^*) - \frac{1}{2} b_{44} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{23} (N_2 - N_2^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{25} (N_2 - N_2^*) (U_2 - U_2^*) - \frac{1}{2} b_{55} (U_2 - U_2^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{34} (T - T^*) (U_1 - U_1^*) - \frac{1}{2} b_{44} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{35} (T - T^*) (U_2 - U_2^*) - \frac{1}{2} b_{55} (U_2 - U_2^*)^2 \end{aligned} \quad (3.26)$$

where

$$\begin{aligned} b_{11} &= \frac{2}{3} \frac{r_{10}}{K_1(T^*)}, \quad b_{22} = \frac{2}{3} b_2 \frac{r_{20}}{K_2(T^*)}, \\ b_{33} &= \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*), \quad b_{44} = (\delta_1 + \nu_1 N_1^*), \quad b_{55} = (\delta_2 + \nu_2 N_2^*), \\ b_{12} &= \beta_1 + b_2 \beta_2, \quad b_{13} = - \left[r_{10} \eta_1(T) N_1 + m_2 (\alpha_1 T - \pi_1 \nu_1 U_1) \right], \\ b_{14} &= \left[\xi_1(U_1) + (\alpha_1 T - \nu_1 U_1) \right], \quad b_{25} = \left[b_2 \xi_2(U_2) + (\alpha_2 T - \nu_2 U_2) \right], \\ b_{23} &= - \left[b_2 r_{20} \eta_2(T) N_2 + (\alpha_2 T - \pi_2 \nu_2 U_2) \right], \\ b_{34} &= \left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right], \quad b_{35} = \left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right] \end{aligned} \quad (3.27)$$

The sufficient conditions for \dot{W} to be negative definite are that the following inequalities hold :

$$\begin{aligned} b_{12}^2 < b_{11}b_{22} , \quad b_{13}^2 < b_{11}b_{33} , \quad b_{14}^2 < b_{11}b_{44} , \quad b_{23}^2 < b_{22}b_{33} , \\ b_{25}^2 < b_{22}b_{55} , \quad b_{34}^2 < b_{33}b_{44} , \quad b_{35}^2 < b_{33}b_{55} . \end{aligned} \quad (3.28)$$

The first condition i.e. $b_{12}^2 < b_{11}b_{22}$ gives

$$\left[\beta_1 + b_2 \beta_2 \right]^2 < \frac{4}{9} b_2 \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)}$$

by choosing $b_2 = \frac{\beta_1}{\beta_2}$ which reduces to

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \text{ which is (3.20a).}$$

The rest of the conditions (3.28) imply (3.20b-g) respectively. Hence W is a Lyapunov's function with respect to \bar{E}_4 whose domain contains the region of attraction Ω_1 , proving the theorem.

4. A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANTS (FOR THE CASE OF CONSTANT EMISSION RATE, i.e. $Q(t) = Q_0$)

In this case, we assume that the dynamics of the environmental and uptake concentrations of the toxicant are so fast such that their equilibria are attained with the densities of both the biological species almost instantaneously. In such a case, we assume :

$$\frac{dT}{dt} \approx 0 \quad \text{and} \quad \frac{dU_i}{dt} \approx 0 \quad \text{for all } t \geq 0 \text{ and for } i = 1, 2.$$

From last three equations of (2.1), we then have,

$$T \approx \frac{Q_0 (\delta_1 + \nu_1 N_1) (\delta_2 + \nu_2 N_2)}{f(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = h(N_1, N_2) \quad (4.1a)$$

$$U_1 \approx \frac{Q_0 \alpha_1 N_1 (\delta_2 + \nu_2 N_2)}{f(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = g_{12}(N_1, N_2) \quad (4.1b)$$

$$U_2 \approx \frac{Q_0 \alpha_2 N_2 (\delta_1 + \nu_1 N_1)}{f(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = g_{21}(N_1, N_2) \quad (4.1c)$$

where $f_1(N_1)$ and $f(N_2)$ are same as defined by (3.3d) and (3.6f) respectively.

We note that T , U_1 and U_2 are expressed as functions of N_1 and N_2 . Then the model (2.1) is reduced to a two dimensional form in N_1 and N_2 and the functions $r_1(U_1)$, $r_2(U_2)$, $K_1(T)$ and $K_2(T)$ are now functions of N_1 and N_2 through (4.1a-c) and they decrease as Q_0 increases and hence $r_1(U_1(N_1, N_2))$, $r_2(U_2(N_1, N_2))$, $K_1(T(N_1, N_2))$ and $K_2(T(N_1, N_2))$ decrease with Q_0 .

The model can finally be written as:

$$\begin{aligned} \frac{dN_1}{dt} &= \left[r_1(U_1(N_1, N_2)) - \frac{r_{10} N_1}{K_1(T(N_1, N_2))} - \beta_1 N_2 \right] N_1 \\ \frac{dN_2}{dt} &= \left[r_2(U_2(N_1, N_2)) - \frac{r_{20} N_2}{K_2(T(N_1, N_2))} - \beta_2 N_1 \right] N_2 \end{aligned} \quad (4.2)$$

with $N_i(0) = N_{i0} \geq 0$, $i = 1, 2$.

The above model (4.2), is a generalized Volterra type competition model where growth rates and carrying capacities are functions of population densities.

To analyze the model (4.2), we note that it has four equilibrium points namely $E_5 = (0, 0)$, $E_6 = (\tilde{N}_1, 0)$, $E_7 = (0, \hat{N}_2)$ and $E_8 = (\tilde{N}_1, \tilde{N}_2)$ where \tilde{N}_1 is the solution of (3.4a), \hat{N}_2 is the solution

of (3.5e) and \tilde{N}_1, \tilde{N}_2 are given by

$$\beta_1 N_2 = r_1(U_1) - r_{10} \frac{N_1}{K_1(T)} \quad (4.3a)$$

$$\beta_2 N_1 = r_2(U_2) - r_{20} \frac{N_2}{K_2(T)} \quad (4.3b)$$

where U_1, U_2 and T are functions of N_1 and N_2 as given in (4.1a-c). The existence and uniqueness of \tilde{N}_1, \tilde{N}_2 can be proved as in previous section under the same set of conditions i.e. under (3.8) and (3.9). We also note that $\tilde{N}_1 < K_{10}, \tilde{N}_2 < K_{20}$ and both \tilde{N}_1, \tilde{N}_2 decrease as Q_0 increases and may even tend to zero.

To show the global stability behavior of $E_8 (\tilde{N}_1, \tilde{N}_2)$, we consider the following positive definite function around E_8 :

$$V_1(N_1, N_2) = (N_1 - \tilde{N}_1 - \tilde{N}_1 \ln \frac{N_1}{\tilde{N}_1}) + (N_2 - \tilde{N}_2 - \tilde{N}_2 \ln \frac{N_2}{\tilde{N}_2})$$

Differentiating V_1 with respect to t along the solution of the model (4.2), we get

$$\begin{aligned} \frac{dV_1}{dt} = & (N_1 - \tilde{N}_1) \left[r_1(U_1(N_1, N_2)) - \frac{r_{10} N_1}{K_1(T(N_1, N_2))} - \beta_1 N_2 \right] \\ & + (N_2 - \tilde{N}_2) \left[r_2(U_2(N_1, N_2)) - \frac{r_{20} N_2}{K_2(T(N_1, N_2))} - \beta_2 N_1 \right] \end{aligned}$$

$$\begin{aligned}
&= (N_1 - \tilde{N}_1) \left[r_1(U_1(N_1, N_2)) - r_1(U_1(\tilde{N}_1, N_2)) + r_1(U_1(\tilde{N}_1, N_2)) \right. \\
&\quad - r_1(U_1(\tilde{N}_1, \tilde{N}_2)) - \frac{r_{10}N_1}{K_1(T(N_1, N_2))} + \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, N_2))} - \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, N_2))} \\
&\quad \left. + \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, \tilde{N}_2))} - \beta_1(N_2 - \tilde{N}_2) \right] \\
&\quad + (N_2 - \tilde{N}_2) \left[r_2(U_2(N_1, N_2)) - r_2(U_2(N_1, \tilde{N}_2)) + r_2(U_2(N_1, \tilde{N}_2)) \right. \\
&\quad - r_2(U_2(\tilde{N}_1, \tilde{N}_2)) - \frac{r_{20}N_2}{K_2(T(N_1, N_2))} + \frac{r_{20}\tilde{N}_2}{K_2(T(N_1, \tilde{N}_2))} - \frac{r_{20}\tilde{N}_2}{K_2(T(N_1, \tilde{N}_2))} \\
&\quad \left. + \frac{r_{20}\tilde{N}_2}{K_2(T(\tilde{N}_1, \tilde{N}_2))} - \beta_2(N_1 - \tilde{N}_1) \right] \\
&= (N_1 - \tilde{N}_1)^2 \left[\xi_{11}(N_1, N_2) - \frac{r_{10}}{K_1(T(N_1, N_2))} - r_{10}\tilde{N}_1 \eta_{11}(N_1, N_2) \right] \\
&\quad + (N_2 - \tilde{N}_2)^2 \left[\xi_{21}(N_1, N_2) - \frac{r_{20}}{K_2(T(N_1, N_2))} - r_{20}\tilde{N}_2 \eta_{21}(N_1, N_2) \right] \\
&\quad + (N_1 - \tilde{N}_1)(N_2 - \tilde{N}_2) \left[\xi_{12}(\tilde{N}_1, N_2) + \xi_{22}(\tilde{N}_1, N_2) - r_{10}\tilde{N}_1 \eta_{12}(\tilde{N}_1, N_2) \right. \\
&\quad \left. - r_{20}\tilde{N}_2 \eta_{22}(\tilde{N}_1, N_2) - (\beta_1 + \beta_2) \right] \tag{4.4}
\end{aligned}$$

where

$$\xi_{i1}(N_1, N_2) = \begin{cases} [r_i(U_i(N_1, N_2)) - r_i(U_i(\tilde{N}_1, N_2))] / (N_1 - \tilde{N}_1), & N_1 \neq \tilde{N}_1 \\ \frac{\partial r_i}{\partial U_i}(U_i(N_1, N_2)) \frac{\partial U_i}{\partial N_1} \Big|_{N_1 = \tilde{N}_1}, & N_1 = \tilde{N}_1 \end{cases},$$

$$\begin{aligned}
\xi_{i2}(\tilde{N}_1, N_2) &= \begin{cases} [r_i(U_i(\tilde{N}_1, N_2)) - r_i(U_i(\tilde{N}_1, \tilde{N}_2))] / (N_2 - \tilde{N}_2), & N_2 \neq \tilde{N}_2 \\ \left. \frac{\partial r_i}{\partial U_i}(U_i(\tilde{N}_1, N_2)) \frac{\partial U_i}{\partial N_2} \right|_{N_2 = \tilde{N}_2}, & N_2 = \tilde{N}_2 \end{cases} \\
\eta_{i1}(N_1, N_2) &= \begin{cases} \frac{\frac{1}{K_i(T(N_1, N_2))} - \frac{1}{K_i(T(\tilde{N}_1, N_2))}}{N_1 - \tilde{N}_1}, & N_1 \neq \tilde{N}_1 \\ - \frac{1}{K_i^2(T(N_1, N_2))} \frac{\partial K_i}{\partial T}(T(N_1, N_2)) \frac{\partial T}{\partial N_1} \Big|_{N_1 = \tilde{N}_1}, & N_1 = \tilde{N}_1 \end{cases} \\
\eta_{i2}(\tilde{N}_1, N_2) &= \begin{cases} \frac{\frac{1}{K_i(T(\tilde{N}_1, N_2))} - \frac{1}{K_i(T(\tilde{N}_1, \tilde{N}_2))}}{N_2 - \tilde{N}_2}, & N_2 \neq \tilde{N}_2 \\ - \frac{1}{K_i^2(T(\tilde{N}_1, N_2))} \frac{\partial K_i}{\partial T}(T(\tilde{N}_1, N_2)) \frac{\partial T}{\partial N_2} \Big|_{N_2 = \tilde{N}_2}, & N_2 = \tilde{N}_2 \end{cases}
\end{aligned} \tag{4.5}$$

Let $r_i(U_i(N_1, N_2))$ and $K_i(T(N_1, N_2))$ satisfy the following conditions

$$\begin{aligned}
K_{mi} &\leq K_i(T(N_1, N_2)) \leq K_{i0}, \quad 0 \leq \xi_{i1}(N_1, N_2) \leq \rho_{i1}, \\
0 &\leq \xi_{i2}(\tilde{N}_1, N_2) \leq \rho_{i2}, \quad 0 \leq \eta_{i1}(N_1, N_2) \leq k_{i1}, \\
0 &\leq \eta_{i2}(\tilde{N}_1, N_2) \leq k_{i2}, \quad i = 1, 2
\end{aligned} \tag{4.6}$$

for some positive constants K_{mi} , ρ_{i1} , ρ_{i2} , k_{i1} and k_{i2} .

From (4.5), (4.6) and the mean value theorem, we note that

$$|\xi_{i1}(N_1, N_2)| \leq \rho_{i1}, \quad |\xi_{i2}(\tilde{N}_1, N_2)| \leq \rho_{i2}, \quad |\eta_{i1}(N_1, N_2)| \leq k_{i1}/K_{mi}^2 \quad \text{and}$$

$$|\eta_{i2}(\tilde{N}_1, N_2)| \leq k_{i2}/K_{mi}^2 \tag{4.7}$$

Now $\frac{dV_1}{dt}$ can further be written as

$$\begin{aligned}
\frac{dV_1}{dt} \leq & - (N_1 - \tilde{N}_1)^2 \left[\frac{r_{10}}{K_{m1}} - \rho_{11} \right] - (N_2 - \tilde{N}_2)^2 \left[\frac{r_{20}}{K_{m2}} - \rho_{21} \right] \\
& + (N_1 - \tilde{N}_1)(N_2 - \tilde{N}_2) \left[\rho_{12} + \rho_{22} - (\beta_1 + \beta_2) \right. \\
& \left. - r_{10}\tilde{N}_1 k_{12}/K_{m1}^2 - r_{20}\tilde{N}_2 k_{22}/K_{m2}^2 \right]
\end{aligned} \tag{4.8}$$

Thus $\frac{dV_1}{dt}$ will be negative definite provided

$$\rho_{11} < \frac{r_{10}}{K_{m1}} \tag{4.9a}$$

$$\rho_{21} < \frac{r_{20}}{K_{m2}} \tag{4.9b}$$

$$\begin{aligned}
& \left[\rho_{12} + \rho_{22} - (\beta_1 + \beta_2) - r_{10}\tilde{N}_1 k_{12}/K_{m1}^2 - r_{20}\tilde{N}_2 k_{22}/K_{m2}^2 \right]^2 \\
& < 4 \left(\frac{r_{10}}{K_{m1}} - \rho_{11} \right) \left(\frac{r_{20}}{K_{m2}} - \rho_{21} \right)
\end{aligned} \tag{4.9c}$$

Hence V_1 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium E_8 $(\tilde{N}_1, \tilde{N}_2)$ and hence this equilibrium is globally asymptotically stable provided the conditions (4.9) are satisfied.

The results in § 3 and § 4 show that if the inequalities (3.20) hold, the competitive species will settle down to its equilibrium level in which the magnitude of competitive species will be lower than their initial carrying capacities and the magnitude of toxicant will depend upon its influx and washout rates. These results also suggest that the outcome of the usual competition in absence of the toxicant, may change because in presence of the toxicant, some of the conditions (3.11), (3.12), (3.13), (3.20), (4.9) may not be satisfied.

5. NUMERICAL EXAMPLE

We give here a numerical example for the model (2.1), in the case of a constant emission rate. The positive equilibrium point i.e. \bar{E}_4 has been computed and the stability conditions (both local and global) i.e conditions (3.13) and (3.20) have been checked and it is found that with the following choice of growth rate and carrying capacity functions and with suitable parameter values, all the conditions are satisfied.

Let us take

$$r_1(U_1) = r_{10} - \frac{a_1 U_1}{1 + r_1 U_1} \quad , \quad r_2(U_2) = r_{20} - \frac{a_2 U_2}{1 + r_2 U_2}$$

$$K_1(T) = K_{10} - \frac{b_1 T}{1 + m_1 T} \quad \text{and} \quad K_2(T) = K_{20} - \frac{b_2 T}{1 + m_2 T} \quad (5.1)$$

where

$$r_{10} = 11.0, \quad r_{20} = 12.0, \quad a_1 = 1.0, \quad a_2 = 1.0, \quad b_1 = 1.0, \quad b_2 = 1.0, \quad r_1 = 2.2, \quad r_2 = 3.2, \quad m_1 = 1.02, \quad m_2 = 1.02, \quad K_{10} = 8.859, \quad K_{20} = 8.859$$

Now with this choice of b_i and m_i , we have $\frac{b_i T}{1 + m_i T} < 1$, $i = 1, 2$

Since $K_{mi} \leq K_i(T) \leq K_{i0}$, therefore we can choose K_{mi} as

$$K_{mi} = 6.5, \quad i = 1, 2.$$

We also note from (5.1) that

$$r'_i(U_i) = - \frac{a_i}{(1 + r_i U_i)^2} \quad \text{and} \quad K'_i(T) = - \frac{b_i}{(1 + m_i T)^2}$$

for $i = 1, 2$

Therefore p_i and q_i can be chosen as 1.0 each ($i = 1, 2$).

Choosing $\pi_1 = 0.05$, $\pi_2 = 0.05$, $\nu_1 = 0.03$, $\nu_2 = 0.03$, $\alpha_1 = 0.02$, $\alpha_2 = 0.02$, $\beta_1 = 0.5$, $\beta_2 = 0.3$, $\delta_0 = 14.0$, $\delta_1 = 15.0$, $\delta_2 = 14.5$, $Q_0 = 5.0$, the equilibrium values N_1^* , N_2^* , T^* , U_1^* and U_2^* are computed as

$N_1^* = 8.596474$, $N_2^* = 8.596643$, $T^* = 0.348826$, $U_1^* = 0.003754$ and $U_2^* = 0.004019$.

6. CONCLUSIONS

In this Chapter, a mathematical model is proposed and analyzed to study the effect of a toxicant emitted in to the environment from an external source on two competing biological species. It is assumed that the uptake concentration of toxicant by each competitor is different and the growth rates of the competitors decrease as the uptake concentration of the toxicant increases. However, the maximum population density of the competitors which the environment can support, is assumed to decrease with the increase in the environmental concentration of the toxicant. It is also considered that the growth rate of each competitor decreases as the density of the other competitor increases. The cases of instantaneous influx of toxicant and a constant influx of toxicant are taken into account. In the case of instantaneous influx of toxicant, it is shown that the competitive species with initial decrease in their densities may recover back to their equilibrium states but after a long time if the washout rate of the toxicant is large. In the case of constant influx of toxicant, it is shown that the competitive species will settle down to their respective equilibrium levels under certain conditions and their magnitudes

will be lower than their initial carrying capacities and the magnitude of the toxicant will depend upon its influx and washout rates. It is also pointed out that the survival of the competitors will be threatened if the constant influx of toxicant continues unabatedly. The analyses also suggests that the usual competition outcome may be altered between the two competing biological species under certain conditions.

CHAPTER - VIII

EXISTENCE AND SURVIVAL OF TWO COMPETING SPECIES UNDER THE HAZARDOUS ACTION OF ONE SPECIES

1. INTRODUCTION

In Chapter VI, we have proposed and analyzed a non linear mathematical model to study the existence and survival of biological species competing with each other under the effect of a toxicant produced by one species and affecting the other, the case of allelopathy. In this Chapter, it is assumed that one of the species produces a toxicant but both the species are affected by this toxicant. This situation exists in aquatic systems (Jorgensen, 1957; Abdul Rahman and Habib, 1989; Chung and Miller, 1995). Using the stability theory of differential equations, the local and global stability behavior of the system is determined. All the other assumptions made in this Chapter are the same as in the previous Chapter VII.

2. MATHEMATICAL MODEL

Consider a closed polluted environment with two competing species. We assume that the toxicant/pollutant is being produced/emitted by one of the species itself and it harms both the biological species. We also assume that both the species have different uptake concentrations of toxicant. Using the similar arguments as Freedman and Shukla (1991), the system is assumed to be governed by following non linear differential equations :

$$\begin{aligned}
\frac{dN_1}{dt} &= r_1(U_1)N_1 - \frac{r_{10}N_1^2}{K_1(T)} - \beta_1N_1N_2 \\
\frac{dN_2}{dt} &= r_2(U_2)N_2 - \frac{r_{20}N_2^2}{K_2(T)} - \beta_2N_1N_2 \\
\frac{dT}{dt} &= \lambda N_1 - \delta_0 T - \alpha_1 N_1 T - \alpha_2 N_2 T + \pi_1 \nu_1 N_1 U_1 + \pi_2 \nu_2 N_2 U_2 \\
\frac{dU_1}{dt} &= -\delta_1 U_1 + \alpha_1 N_1 T - \nu_1 N_1 U_1 \\
\frac{dU_2}{dt} &= -\delta_2 U_2 + \alpha_2 N_2 T - \nu_2 N_2 U_2 \\
N_1(0) &= N_{10} \geq 0, N_2(0) = N_{20} \geq 0, T(0) = T_0 = cN_{10} \geq 0, \\
U_1(0) &= c_1 T_0, U_2(0) = c_2 T_0, c > 0, c_1 > 0, c_2 > 0, \\
0 &\leq \pi_1 \leq 1, 0 \leq \pi_2 \leq 1.
\end{aligned} \tag{2.1}$$

Here $N_i(t)$ ($i = 1, 2$) is the density of the i -th competing species, λ is a positive constant, which denotes the rate of production coefficient of toxicant with an environmental concentration $T(t)$ by one of the biological species (here, we label this biological species with biomass density as $N_1(t)$). $U_i(t)$ is the uptake concentration of toxicant by the i -th species, $\delta_0 > 0$ is the natural washout rate coefficient of $T(t)$, $\alpha_i > 0$ is the depletion rate coefficient of $T(t)$ due to its uptake by the i -th species, $\delta_i > 0$ is the natural washout rate coefficient of $U_i(t)$, $\nu_i > 0$ is the depletion rate coefficient of $U_i(t)$ due to decay of some members of $N_i(t)$ and a fraction π_i of which may reenter into the environment, $c_i \geq 0$ is the proportionality constant determining the measure of initial toxicant concentration in the i -th species at $t = 0$, where $i = 1, 2$. It is assumed in modelling the system (2.1) that the

growth rate of uptake concentration $U_i(t)$ increases with $\alpha_i N_i T$ which denotes the rate of depletion of the toxicant in the environment due to its uptake by the i -th species. The constants β_1 and β_2 are competition coefficients and are assumed to be positive. The constants c , c_1 and c_2 are positive.

In our model (2.1), the function $r_i(U_i)$ denotes the growth rate coefficient of i -th species which decreases with U_i and hence we assume that

$$r_i(0) = r_{i0} > 0, \quad \frac{dr_i}{dU_i} < 0 \quad \text{for } U_i > 0, \quad i = 1, 2 \quad (2.2)$$

Similarly the function $K_i(T)$ denotes the maximum population density of the i -th species which the environment can support and it also decreases with T and hence we assume that

$$K_i(0,0) = K_{i0} > 0, \quad \frac{dK_i}{dT} < 0 \quad \text{for } T > 0, \quad i = 1, 2 \quad (2.3)$$

3. MATHEMATICAL ANALYSIS

The model (2.1) has four nonnegative equilibria, namely $E_1(0,0,0,0,0)$, $E_2(\tilde{N}_1, 0, \tilde{T}, \tilde{U}_1, 0)$, $E_3(0, K_{20}, 0, 0, 0)$ and $E_4(N_1^*, N_2^*, T^*, U_1^*, U_2^*)$. The existence of E_1 or E_3 is obvious. We shall show the existence of E_2 and E_4 as follows.

EXISTENCE OF E_2 :

Here \tilde{N}_1 , \tilde{T} and \tilde{U}_1 are the positive solution of the system of equations

$$N_1 = \frac{r_1(U_1) K_1(T)}{r_{10}} \quad (3.1a)$$

$$T = \frac{\lambda N_1 (\delta_1 + \nu_1 N_1)}{f_1(N_1)} = h(N_1) \quad (3.1b)$$

$$U_1 = \frac{\lambda \alpha_1 N_1^2}{f_1(N_1)} = g(N_1) \quad (3.1c)$$

$$\text{where } f_1(N_1) = \delta_0 \delta_1 + (\delta_0 \nu_1 + \alpha_1 \delta_1) N_1 + \alpha_1 \nu_1 (1 - \pi_1) N_1^2 \quad (3.1d)$$

We note that as λ increases, both T and U_1 , increase. Thus, $r_1(U_1)$ and $K_1(T)$ decrease as λ increases making \tilde{N}_1 to decrease.

$$\text{Letting } F(N_1) = r_{10} N_1 - r_1(g(N_1)) K_1(h(N_1)) \quad (3.1e),$$

we note that

$$F(0) < 0 \text{ and } F(K_{10}) > 0.$$

This guarantees the existence of a root of $F(N_1) = 0$ for $0 < N_1 < K_{10}$, say \tilde{N}_1 . Further, this root will be unique provided

$$F'(N_1) = r_{10} - \left\{ r_1 \frac{dK_1}{dT} \frac{dh}{dN_1} + K_1 \frac{dr_1}{dU_1} \frac{dg}{dN_1} \right\} > 0 \quad (3.1f)$$

Knowing the value of \tilde{N}_1 , the values of \tilde{T} and \tilde{U}_1 can be computed from equations (3.1b) and (3.1c).

EXISTENCE OF E_4 :

Here

$$\beta_1 N_2 = r_1(U_1) - r_{10} \frac{N_1}{K_1(T)} \quad (3.2a)$$

$$\beta_2 N_1 = r_2(U_2) - r_{20} \frac{N_2}{K_2(T)} \quad (3.2b)$$

$$T = \frac{\lambda N_1 (\delta_1 + \nu_1 N_1) (\delta_2 + \nu_2 N_2)}{f_2(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = h_1(N_1, N_2) \quad (3.2c)$$

$$U_1 = \frac{\lambda \alpha_1 N_1^2 (\delta_2 + \nu_2 N_2)}{f_2(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = g_1(N_1, N_2) \quad (3.2d)$$

$$U_2 = \frac{\lambda \alpha_2 N_2^2 (\delta_1 + \nu_1 N_1)}{f_2(N_2) (\delta_1 + \nu_1 N_1) + f_1(N_1) (\delta_2 + \nu_2 N_2)} = g_2(N_1, N_2) \quad (3.2e)$$

here $f_1(N_1)$ is the same as defined by (3.1d) and

$$f_2(N_2) = \alpha_2 \delta_2 N_2 + \alpha_2 \nu_2 (1 - \pi_2) N_2^2 \quad (3.2f)$$

From (3.2c-e), we note that as λ increases, T , U_1 and U_2 increase. Thus, $r_1(U_1)$, $r_2(U_2)$, $K_1(T)$ and $K_2(T)$ decrease as λ increases making N_1^* , N_2^* to decrease. (see equations (3.3a,b)).

$$\text{Let } F_1(N_1, N_2) = [r_1(g_1) - \beta_1 N_2] K_1(h_1) - r_{10} N_1 \quad (3.3a)$$

$$\text{and } F_2(N_1, N_2) = [r_2(g_2) - \beta_2 N_1] K_2(h_1) - r_{20} N_2 \quad (3.3b)$$

For the existence of N_1^* , N_2^* , the two curves given by

$$F_1(N_1, N_2) = 0 \quad (I)$$

$$\text{and } F_2(N_1, N_2) = 0 \quad (II)$$

must intersect.

We note

$$F_1(0, 0) = r_{10} K_{10} > 0 \quad \text{and} \quad F_2(0, 0) = r_{20} K_{20} > 0.$$

$$\text{Also, } F_1(0, N_2) = 0 \implies N_2 = \frac{r_{10}}{\beta_1}, \quad F_1(N_1, 0) = 0 \implies N_1 = \tilde{N}_1,$$

$$F_2(0, N_2) = 0 \implies N_2 = K_{20}, \quad F_2(N_1, 0) = 0 \implies N_1 = \frac{r_{20}}{\beta_2}.$$

Where \tilde{N}_1 and K_{20} are the equilibrium values in E_2 and E_3 .

Thus, both the curves (I) and (II) intersect each other in the region $R = \left\{ (N_1, N_2) : 0 \leq N_1 \leq \frac{r_{20}}{\beta_2}, 0 \leq N_2 \leq \frac{r_{10}}{\beta_1} \right\}$ provided

the following inequalities hold under the two cases: (see Fig. (1))

$$\text{Case (i)} \quad \frac{r_{10}}{\beta_1} > K_{20} , \quad \frac{r_{20}}{\beta_2} > \tilde{N}_1 \quad \text{or}$$

$$\text{Case (ii)} \quad \frac{r_{10}}{\beta_1} < K_{20} , \quad \frac{r_{20}}{\beta_2} < \tilde{N}_1 \quad (3.4)$$

For uniqueness of this point of intersection, (N_1^*, N_2^*) , we must have $\frac{dN_2}{dN_1} < 0$ for both the curves in R.

For curve (I),

$$\frac{dN_2}{dN_1} = \frac{r_{10} - K_1(h_1) \frac{dr_1}{dU_1} \frac{\partial g_1}{\partial N_1} - \left(r_1(g_1) - \beta_1 N_2 \right) \frac{dK_1}{dT} \frac{\partial h_1}{\partial N_1}}{K_1(h_1) \left(\frac{dr_1}{dU_1} \frac{\partial g_1}{\partial N_2} - \beta_1 \right) + \left(r_1(g_1) - \beta_1 N_2 \right) \frac{dK_1}{dT} \frac{\partial h_1}{\partial N_2}} \quad (3.5a)$$

and for curve (II),

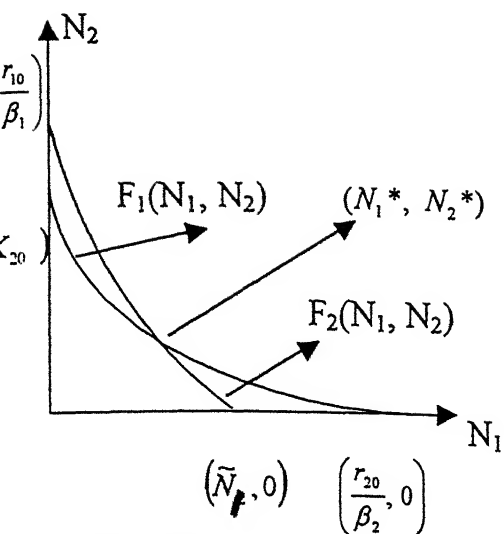
$$\frac{dN_2}{dN_1} = \frac{K_2(h_1) \left(\frac{dr_2}{dU_2} \frac{\partial g_2}{\partial N_1} - \beta_2 \right) + \left(r_2(g_2) - \beta_2 N_1 \right) \frac{dK_2}{dT} \frac{\partial h_1}{\partial N_1}}{r_{20} - K_2(h_1) \frac{dr_2}{dU_2} \frac{\partial g_2}{\partial N_2} - \left(r_2(g_2) - \beta_2 N_1 \right) \frac{dK_2}{dT} \frac{\partial h_1}{\partial N_2}} \quad (3.5b)$$

In case (i), the absolute value of $\frac{dN_2}{dN_1}$ given by (3.5a) is less than the absolute value of $\frac{dN_2}{dN_1}$ given by (3.5b). For the case (ii), the opposite thing occurs.

Knowing the values of N_1^*, N_2^* ; T^*, U_1^* and U_2^* can be computed from equations (3.2c) - (3.2e).

STABILITY ANALYSIS

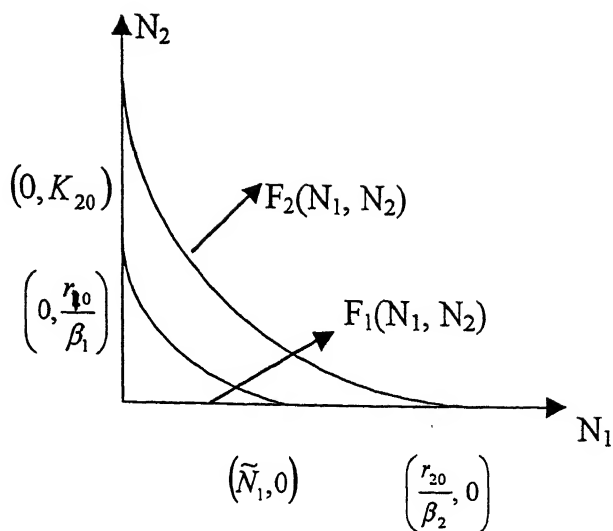
To study the local stability behavior of the equilibria, we compute the variational matrices corresponding to the equilibria. Let M_i be the variational matrix corresponding to the equilibria E_i , then we have,



Case when

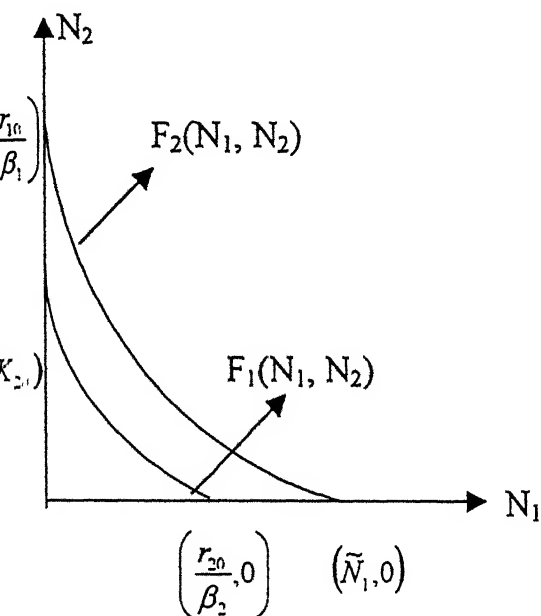
$$\tilde{N}_1 < \frac{r_{20}}{\beta_2}, \quad K_{20} < \frac{r_{10}}{\beta_1}$$

Case (i)



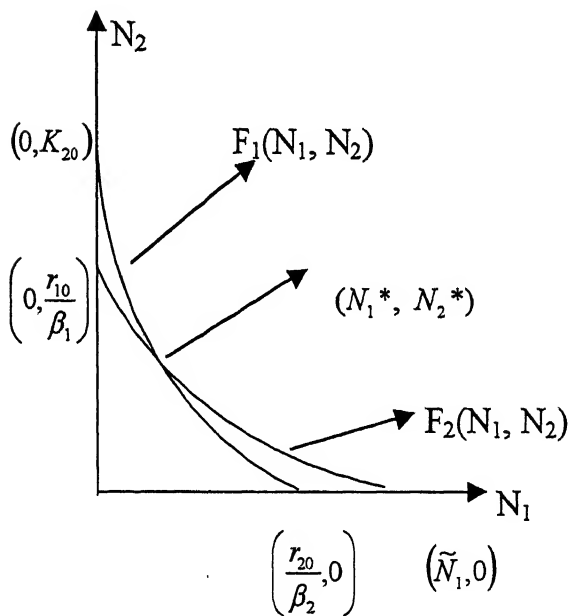
Case when

$$\tilde{N}_1 < \frac{r_{20}}{\beta_2}, \quad K_{20} > \frac{r_{10}}{\beta_1}$$



Case when

$$\tilde{N}_1 > \frac{r_{20}}{\beta_2}, \quad \tilde{N}_2 < \frac{r_{10}}{\beta_1}$$



Case when,

$$\tilde{N}_1 > \frac{r_{20}}{\beta_2}, \quad \tilde{N}_2 > \frac{r_{10}}{\beta_1}$$

Case (ii)

Fig (1)

$$M_1 = \begin{bmatrix} r_{10} & 0 & 0 & 0 & 0 \\ 0 & r_{20} & 0 & 0 & 0 \\ \lambda & 0 & -\delta_0 & 0 & 0 \\ 0 & 0 & 0 & -\delta_1 & 0 \\ 0 & 0 & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$M_2 = \begin{bmatrix} -r_1(\tilde{U}_1) & -\beta_1 \tilde{N}_1 & G_{11} & r'_1(\tilde{U}_1) \tilde{N}_1 & 0 \\ 0 & r_{20} - \beta_2 \tilde{N}_1 & 0 & 0 & 0 \\ \lambda - (\alpha_1 \tilde{T} - \pi_1 \nu_1 \tilde{U}_1) & -\alpha_2 \tilde{T} & -(\delta_0 + \alpha_1 \tilde{N}_1) & \pi_1 \nu_1 \tilde{N}_1 & 0 \\ \alpha_1 \tilde{T} - \nu_1 \tilde{U}_1 & 0 & \alpha_1 \tilde{N}_1 & -(\delta_1 + \nu_1 \tilde{N}_1) & 0 \\ 0 & \alpha_2 \tilde{T} & 0 & 0 & -\delta_2 \end{bmatrix}$$

$$M_3 = \begin{bmatrix} r_{10} - \beta_1 K_{20} & 0 & 0 & 0 & 0 \\ -\beta_2 K_{20} & -r_{20} & r_{20} K'_2(0) & 0 & r'_2(0) K_{20} \\ \lambda & 0 & -(\delta_0 + \alpha_2 K_{20}) & 0 & \pi_2 \nu_2 K_{20} \\ 0 & 0 & 0 & -\delta_1 & 0 \\ 0 & 0 & \alpha_2 K_{20} & 0 & -(\delta_2 + \nu_2 K_{20}) \end{bmatrix}$$

$$M_4 = \begin{bmatrix} -\frac{r_{10}N_1^*}{K_1(T^*)} & -\beta_1N_1^* & G_{21} & r_1'(U_1^*)N_1^* & 0 \\ -\beta_2N_2^* & -\frac{r_{20}N_2^*}{K_2(T^*)} & G_{22} & 0 & r_2'(U_2^*)N_2^* \\ G_{31} & G_{32} & -(\delta_0 + \alpha_1N_1^* + \alpha_2N_2^*) & \pi_1\nu_1N_1^* & \pi_2\nu_2N_2^* \\ G_{41} & 0 & \alpha_1N_1^* & -(\delta_1 + \nu_1N_1^*) & 0 \\ 0 & G_{42} & \alpha_2N_2^* & 0 & -(\delta_2 + \nu_2N_2^*) \end{bmatrix}$$

Where

$$\begin{aligned} G_{11} &= \frac{r_1^2(\tilde{U}_1)}{r_{10}} K_1'(\tilde{T}) , \\ G_{21} &= \frac{r_{10}N_1^{*2}}{K_1^2(T^*)} K_1'(T^*) , \quad G_{22} = \frac{r_{20}N_2^{*2}}{K_2^2(T^*)} K_2'(T^*) , \\ G_{31} &= \lambda - (\alpha_1T^* - \pi_1\nu_1U_1^*) , \quad G_{32} = -(\alpha_2T^* - \pi_2\nu_2U_2^*) , \\ G_{41} &= \alpha_1T^* - \nu_1U_1^* , \quad G_{42} = \alpha_2T^* - \nu_2U_2^* \end{aligned} \quad (3.6)$$

From M_1 , we note that E_1 is a saddle point with unstable manifold locally in N_1 - N_2 space and stable manifold locally in T - U_1 - U_2 space.

From M_2 , it can be checked that E_2 is locally asymptotically stable provided

$$\frac{r_{20}}{\beta_2} < \tilde{N}_1 \quad (3.7)$$

Otherwise, it is unstable.

From M_3 , we note that E_3 is locally asymptotically stable provided

$$\frac{r_{10}}{\beta_1} < K_{20} \quad (3.8)$$

Otherwise, it is unstable.

We can not make any obvious remark about E_4 from M_4 . Hence we use Lyapunov's stability theorem to study the stability behavior of E_4 . In the following theorem we are able to find sufficient conditions under which E_4 is locally asymptotically stable.

THEOREM 3.1 Let the following inequalities hold:

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \quad (3.9a)$$

$$\left[\frac{r_{10} N_1^*}{K_1^2(T^*)} K_1'(T^*) + \left(\lambda - \alpha_1 T^* + \pi_1 \nu_1 U_1^* \right) \right]^2 < \frac{1}{3} \frac{r_{10}}{K_1(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.9b)$$

$$\left[r_1'(U_1^*) + \left(\alpha_1 T^* - \nu_1 U_1^* \right) \right]^2 < \frac{2}{3} \frac{r_{10}}{K_1(T^*)} (\delta_1 + \nu_1 N_1^*) \quad (3.9c)$$

$$\left[\left(\alpha_2 T^* - \pi_2 \nu_2 U_2^* \right) - \frac{\beta_1}{\beta_2} \frac{r_{20} N_2^*}{K_2^2(T^*)} K_2'(T^*) \right]^2 < \frac{1}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.9d)$$

$$\left[\frac{\beta_1}{\beta_2} r_2'(U_2^*) + b_4 \left(\alpha_2 T^* - \nu_2 U_2^* \right) \right]^2 < \frac{2}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_2 + \nu_2 N_2^*) \quad (3.9e)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_1 + \nu_1 N_1^*) \quad (3.9f)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_2 + \nu_2 N_2^*) \quad (3.9g)$$

Then E_4 is locally asymptotically stable in case (i).

PROOF: In order to prove the local asymptotic stability of E_4 , let us take the following perturbations around the equilibrium E_4 :

$N_1 = N_1^* + n_1$, $N_2 = N_2^* + n_2$, $T = T^* + \tau$, $U_1 = U_1^* + u_1$, $U_2 = U_2^* + u_2$ where n_1 , n_2 , τ , u_1 , u_2 are small perturbations from E_4 .

Then the linearized system of (2.1)

$$\begin{aligned}\dot{n}_1 &= - \frac{r_{10}N_1^*}{K_1(T^*)} n_1 - \beta_1 N_1^* n_2 + \frac{r_{10}N_1^*}{K_1^2(T^*)} K_1'(T^*) \tau + r_1'(U_1^*) N_1^* u_1 \\ \dot{n}_2 &= - \beta_2 N_2^* n_1 - \frac{r_{20}N_2^*}{K_2(T^*)} n_2 + \frac{r_{20}N_2^*}{K_2^2(T^*)} K_2'(T^*) \tau + r_2'(U_2^*) N_2^* u_2 \\ \dot{\tau} &= \left[\lambda - (\alpha_1 T^* - \pi_1 \nu_1 U_1^*) \right] n_1 - (\alpha_2 T^* - \pi_2 \nu_2 U_2^*) n_2 \\ &\quad - (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \tau + \pi_1 \nu_1 N_1^* u_1 + \pi_2 \nu_2 N_2^* u_2 \\ \dot{u}_1 &= (\alpha_1 T^* - \nu_1 U_1^*) n_1 + \alpha_1 N_1^* \tau - (\delta_1 + \nu_1 N_1^*) u_1 \\ \dot{u}_2 &= (\alpha_2 T^* - \nu_2 U_2^*) n_2 + \alpha_2 N_2^* \tau - (\delta_2 + \nu_2 N_2^*) u_2\end{aligned}\tag{3.10}$$

Now consider the following positive definite function

$$V = \frac{1}{2} n_1^2 + \frac{1}{2} b_1 n_2^2 + \frac{1}{2} \tau^2 + \frac{1}{2} u_1^2 + \frac{1}{2} u_2^2\tag{3.11}$$

$$\text{Then } \dot{V} = n_1 \dot{n}_1 + b_1 n_2 \dot{n}_2 + \tau \dot{\tau} + u_1 \dot{u}_1 + u_2 \dot{u}_2$$

Substituting values of \dot{n}_1 , \dot{n}_2 , $\dot{\tau}$, \dot{u}_1 and \dot{u}_2 from (3.10) in to this equation and with a little algebraic manipulation, we get

$$\begin{aligned}
\dot{V} = & -\frac{1}{2} a_{11} n_1^2 + a_{12} n_1 n_2 - \frac{1}{2} a_{22} n_2^2 \\
& -\frac{1}{2} a_{11} n_1^2 + a_{13} n_1 \tau - \frac{1}{2} a_{33} \tau^2 \\
& -\frac{1}{2} a_{11} n_1^2 + a_{14} n_1 u_1 - \frac{1}{2} a_{44} u_1^2 \\
& -\frac{1}{2} a_{22} n_2^2 + a_{23} n_2 \tau - \frac{1}{2} a_{33} \tau^2 \\
& -\frac{1}{2} a_{22} n_2^2 + a_{25} n_2 u_2 - \frac{1}{2} a_{55} u_2^2 \\
& -\frac{1}{2} a_{33} \tau^2 + a_{34} \tau u_1 - \frac{1}{2} a_{44} u_1^2 \\
& -\frac{1}{2} a_{33} \tau^2 + a_{35} \tau u_2 - \frac{1}{2} a_{55} u_2^2
\end{aligned} \tag{3.12}$$

$$\text{where } a_{11} = \frac{2}{3} \frac{r_{10}}{K_1(T^*)}, \quad a_{22} = \frac{2}{3} b_1 \frac{r_{20}}{K_2(T^*)},$$

$$a_{33} = \frac{1}{2} b_2 (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*), \quad a_{44} = b_3 (\delta_1 + \nu_1 N_1^*), \quad a_{55} = b_4 (\delta_2 + \nu_2 N_2^*),$$

$$a_{12} = \beta_1 + b_1 \beta_2, \quad a_{13} = \left(\lambda - \alpha_1 T^* + \pi_1 \nu_1 U_1^* \right) + \frac{r_{10} N_1^*}{K_1^2(T^*)} K_1'(T^*),$$

$$a_{14} = r_1'(U_1^*) + \left(\alpha_1 T^* - \nu_1 U_1^* \right), \quad a_{25} = b_1 r_2'(U_2^*) + \left(\alpha_2 T^* - \nu_2 U_2^* \right),$$

$$a_{23} = \left(\alpha_2 T^* - \pi_2 \nu_2 U_2^* \right) - b_1 \frac{r_{20} N_2^*}{K_2^2(T^*)} K_2'(T^*),$$

$$a_{34} = (\pi_1 \nu_1 + \alpha_1) N_1^*, \quad a_{35} = (\pi_2 \nu_2 + \alpha_2) N_2^* \tag{3.13}$$

From (3.12) and (3.13) we note that \dot{V} will be negative definite provided

$$\begin{aligned}
a_{12}^2 & < a_{11} a_{22}, \quad a_{13}^2 < a_{11} a_{33}, \quad a_{14}^2 < a_{11} a_{44}, \quad a_{23}^2 < a_{22} a_{33}, \\
a_{25}^2 & < a_{22} a_{55}, \quad a_{34}^2 < a_{33} a_{44}, \quad a_{35}^2 < a_{33} a_{55},
\end{aligned} \tag{3.14}$$

The first condition i.e. $a_{12}^2 < a_{11} a_{22}$ gives

$$\left[\beta_1 + b_1 \beta_2 \right]^2 < \frac{4}{9} b_1 \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)}$$

by choosing $b_1 = \frac{\beta_1}{\beta_2}$, this reduces to

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \text{ which is (3.9a).}$$

The rest of the conditions (3.14) respectively imply the conditions (3.9b-g). This shows that under the conditions (3.9) \dot{V} is negative definite showing that V is a Lyapunov's function for the linearized system and hence the proof of the theorem (3.1) follows.

In the following theorem we have shown that E_4 is globally asymptotically stable. To prove this theorem we first give the following lemma without proof which establishes a region of attraction for our system (2.1).

LEMMA 3.1 The set

$$\Omega = \left\{ (N_1, N_2, T, U_1, U_2) : 0 \leq N_1 \leq K_{10}, 0 \leq N_2 \leq K_{20}, \right. \\ \left. 0 \leq T + U_1 + U_2 \leq \frac{\lambda K_{10}}{\delta} \right\}, \text{ where } \delta = \min(\delta_0, \delta_1, \delta_2)$$

attracts all solutions initiating in the positive orthant.

THEOREM 3.2 In addition to the assumptions (2.2) and (2.3), let

$r_i(U_i)$ and $K_i(T)$ satisfy in Ω :

$$K_{mi} \leq K(T) \leq K_{i0}, \quad 0 \leq -r'_i(U_i) \leq p_i, \quad 0 \leq -K'_i(T) \leq q_i \\ \text{for } i = 1, 2 \quad (3.15)$$

for some positive constants K_{mi} , p_i and q_i .

Then if the following inequalities hold :

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \quad (3.16a)$$

$$\left[\frac{r_{10} q_1 K_{10}}{K_{m1}^2} + (\lambda + \alpha_1 + \pi_1 \nu_1) \frac{\lambda K_{10}}{\delta} \right]^2 < \frac{1}{3} \frac{r_{10}}{K_1(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.16b)$$

$$\left[p_1 + (\alpha_1 + \nu_1) \frac{\lambda K_{10}}{\delta} \right]^2 < \frac{2}{3} \frac{r_{10}}{K_1(T^*)} (\delta_1 + \nu_1 N_1^*) \quad (3.16c)$$

$$\left[\frac{\beta_1}{\beta_2} \frac{r_{20} q_2 K_{20}}{K_{m2}^2} + (\alpha_2 + \pi_2 \nu_2) \frac{\lambda K_{10}}{\delta} \right]^2 < \frac{1}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) \quad (3.16d)$$

$$\left[\frac{\beta_1}{\beta_2} p_2 + (\alpha_2 + \nu_2) \frac{\lambda K_{10}}{\delta} \right]^2 < \frac{2}{3} \frac{\beta_1}{\beta_2} \frac{r_{20}}{K_2(T^*)} (\delta_2 + \nu_2 N_2^*) \quad (3.16e)$$

$$\left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_1 + \nu_1 N_1^*) \quad (3.16f)$$

$$\left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right]^2 < \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (\delta_2 + \nu_2 N_2^*) \quad (3.16g)$$

E_4 is globally asymptotically stable in Ω in case (i).

PROOF: We consider the following positive definite function about E_4 ,

$$\begin{aligned} W(N_1, N_1^*, T, U_1, U_1^*) &= \left(N_1 - N_1^* - N_1^* \ln \frac{N_1}{N_1^*} \right) \\ &+ b_2 \left(N_2 - N_2^* - N_2^* \ln \frac{N_2}{N_2^*} \right) \\ &+ \frac{1}{2} (T - T^*)^2 + \frac{1}{2} (U_1 - U_1^*)^2 + \frac{1}{2} (U_2 - U_2^*)^2 \quad (3.17) \end{aligned}$$

Differentiating W with respect to t along the solution of (2.1), we get

$$\begin{aligned}
\dot{W} = & (N_1 - N_1^*) \left[r_1(U_1) - \frac{r_{10}N_1}{K_1(T)} - \beta_1 N_2 \right] \\
& + b_2 (N_2 - N_2^*) \left[r_2(U_2) - \frac{r_{20}N_2}{K_2(T)} - \beta_2 N_1 \right] \\
& + (T - T^*) \left[\lambda N_1 - \delta_0 T - \alpha_1 N_1 T - \alpha_2 N_2 T + \pi_1 \nu_1 N_1 U_1 + \pi_2 \nu_2 N_2 U_2 \right] \\
& + (U_1 - U_1^*) \left[-\delta_1 U_1 + \alpha_1 N_1 T - \nu_1 N_1 U_1 \right] \\
& + (U_2 - U_2^*) \left[-\delta_2 U_2 + \alpha_2 N_2 T - \nu_2 N_2 U_2 \right]
\end{aligned} \tag{3.18}$$

using (3.2), a little algebraic manipulation yields,

$$\begin{aligned}
\dot{W} = & - \frac{r_{10}}{K_1(T^*)} (N_1 - N_1^*)^2 - b_2 \frac{r_{20}}{K_2(T^*)} (N_2 - N_2^*)^2 \\
& - (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*) (T - T^*)^2 - (\delta_1 + \nu_1 N_1^*) (U_1 - U_1^*)^2 \\
& - (\delta_2 + \nu_2 N_2^*) (U_2 - U_2^*)^2 \\
& + (N_1 - N_1^*) (N_2 - N_2^*) \left[\beta_1 + b_2 \beta_2 \right] \\
& + (N_1 - N_1^*) (T - T^*) \left[-r_{10} \eta_1(T) N_1 + \left\{ \lambda - (\alpha_1 T - \pi_1 \nu_1 U_1) \right\} \right] \\
& + (N_1 - N_1^*) (U_1 - U_1^*) \left[\xi_1(U_1) + (\alpha_1 T - \nu_1 U_1) \right] \\
& + (N_2 - N_2^*) (T - T^*) \left[-b_2 r_{20} \eta_2(T) N_2 - (\alpha_2 T - \pi_2 \nu_2 U_2) \right] \\
& + (N_2 - N_2^*) (U_2 - U_2^*) \left[b_2 \xi_2(U_2) + (\alpha_2 T - \nu_2 U_2) \right] \\
& + (T - T^*) (U_1 - U_1^*) \left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right] \\
& + (T - T^*) (U_2 - U_2^*) \left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right]
\end{aligned} \tag{3.19}$$

where

$$\xi_i(U_i) = \begin{cases} \frac{r_i(U_i) - r_i(U_i^*)}{(U_i - U_i^*)}, & U_i \neq U_i^* \\ r'_i(U_i^*) & , \quad U_i = U_i^* \end{cases}$$

$$\eta_i(T) = \begin{cases} \left[\frac{1}{K_i(T)} - \frac{1}{K_i(T^*)} \right] / (T - T^*), & T \neq T^* \\ - \frac{K'_i(T^*)}{K_i^2(T^*)} & , \quad T = T^* \end{cases}$$

(3.20)

using (3.20) and mean value theorem, we get

$$|\xi_i(U_i)| \leq p_i, \quad |\eta_i(T)| \leq q_i/K_{mi}^2 \quad \text{for } i = 1, 2. \quad (3.21)$$

\dot{W} can further be written as sum of the quadratics,

$$\begin{aligned} \dot{W} = & -\frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{12} (N_1 - N_1^*) (N_2 - N_2^*) - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 \\ & - \frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{13} (N_1 - N_1^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{11} (N_1 - N_1^*)^2 + b_{14} (N_1 - N_1^*) (U_1 - U_1^*) - \frac{1}{2} b_{44} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{23} (N_2 - N_2^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{22} (N_2 - N_2^*)^2 + b_{25} (N_2 - N_2^*) (U_2 - U_2^*) - \frac{1}{2} b_{55} (U_2 - U_2^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{34} (T - T^*) (U_1 - U_1^*) - \frac{1}{2} b_{44} (U_1 - U_1^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{35} (T - T^*) (U_2 - U_2^*) - \frac{1}{2} b_{55} (U_2 - U_2^*)^2 \end{aligned}$$

(3.22)

where

$$b_{11} = \frac{2}{3} \frac{r_{10}}{K_1(T^*)}, \quad b_{22} = \frac{2}{3} b_2 \frac{r_{20}}{K_2(T^*)},$$

$$b_{33} = \frac{1}{2} (\delta_0 + \alpha_1 N_1^* + \alpha_2 N_2^*), \quad b_{44} = (\delta_1 + \nu_1 N_1^*), \quad b_{55} = (\delta_2 + \nu_2 N_2^*),$$

$$\begin{aligned}
b_{12} &= \beta_1 + b_2 \beta_2, \quad b_{13} = - \left[r_{10} \eta_1(T) N_1 + \left\{ \lambda - (\alpha_1 T - \pi_1 \nu_1 U_1) \right\} \right], \\
b_{14} &= \left[\xi_1(U_1) + (\alpha_1 T - \nu_1 U_1) \right], \quad b_{25} = \left[b_2 \xi_2(U_2) + (\alpha_2 T - \nu_2 U_2) \right], \\
b_{23} &= - \left[b_2 r_{20} \eta_2(T) N_2 + (\alpha_2 T - \pi_2 \nu_2 U_2) \right], \quad b_{34} = \left[(\pi_1 \nu_1 + \alpha_1) N_1^* \right] \\
\text{and } b_{35} &= \left[(\pi_2 \nu_2 + \alpha_2) N_2^* \right] \tag{3.23}
\end{aligned}$$

From (3.22), we note that the sufficient conditions for \dot{W} to be negative definite are that the following inequalities hold :

$$\begin{aligned}
b_{12}^2 &< b_{11} b_{22}, \quad b_{13}^2 < b_{11} b_{33}, \quad b_{14}^2 < b_{11} b_{44}, \quad b_{23}^2 < b_{22} b_{33}, \\
b_{25}^2 &< b_{22} b_{55}, \quad b_{34}^2 < b_{33} b_{44}, \quad b_{35}^2 < b_{33} b_{55} \tag{3.24}
\end{aligned}$$

The first condition i.e. $b_{12}^2 < b_{11} b_{22}$ gives

$$\left[\beta_1 + b_2 \beta_2 \right]^2 < \frac{4}{9} b_2 \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)}$$

by choosing $b_2 = \frac{\beta_1}{\beta_2}$, the above condition reduces to

$$\beta_1 \beta_2 < \frac{1}{9} \frac{r_{10}}{K_1(T^*)} \frac{r_{20}}{K_2(T^*)} \text{ which is (3.16a).}$$

The rest of the conditions (3.24) imply (3.16b-g) respectively.

Hence W is a Lyapunov function with respect to E_4 whose domain contains the region of attraction Ω , proving the theorem.

4. A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANTS

In this case, we assume that the dynamics of the environmental and uptake concentrations of the toxicant are so fast, that their equilibria are attained with the densities of both the biological

To analyze the model (4.2), we note that it has four equilibrium points namely $E_5 = (0,0)$, $E_6 = (\tilde{N}_1, 0)$, $E_7 = (0, K_{20})$ and $E_8 = (\tilde{\tilde{N}}_1, \tilde{\tilde{N}}_2)$ where \tilde{N}_1 is the solution of (3.1e) and $\tilde{\tilde{N}}_1, \tilde{\tilde{N}}_2$ are solutions of the following algebraic equations:

$$\beta_1 N_2 = r_1(U_1) - r_{10} \frac{N_1}{K_1(T)} \quad (4.3a)$$

$$\beta_2 N_1 = r_2(U_2) - r_{20} \frac{N_2}{K_2(T)} \quad (4.3b)$$

where U_1, U_2 and T are functions of N_1 and N_2 as given in (4.1a-c). The existence and uniqueness of $\tilde{\tilde{N}}_1, \tilde{\tilde{N}}_2$ can be proved as in previous section under the same set of conditions i.e. under (3.4) and (3.5).

We also note that $\tilde{\tilde{N}}_1 < K_{10}, \tilde{\tilde{N}}_2 < K_{20}$ and both $\tilde{\tilde{N}}_1, \tilde{\tilde{N}}_2$ decrease as λ increases and may even tend to zero.

To show the global stability behavior of E_8 we consider the following positive definite function around E_8 :

$$V_1(N_1, N_2) = (N_1 - \tilde{\tilde{N}}_1 - \tilde{\tilde{N}}_1 \ln \frac{N_1}{\tilde{\tilde{N}}_1}) + (N_2 - \tilde{\tilde{N}}_2 - \tilde{\tilde{N}}_2 \ln \frac{N_2}{\tilde{\tilde{N}}_2})$$

Differentiating V_1 with respect to t along the solution of the model (4.2), we get

$$\begin{aligned} \frac{dV_1}{dt} = & (N_1 - \tilde{\tilde{N}}_1) \left[r_1(U_1(N_1, N_2)) - \frac{r_{10} N_1}{K_1(T(N_1, N_2))} - \beta_1 N_2 \right] \\ & + (N_2 - \tilde{\tilde{N}}_2) \left[r_2(U_2(N_1, N_2)) - \frac{r_{20} N_2}{K_2(T(N_1, N_2))} - \beta_2 N_1 \right] \end{aligned}$$

$$\begin{aligned}
&= (N_1 - \tilde{N}_1) \left[r_1(U_1(N_1, N_2)) - r_1(U_1(\tilde{N}_1, N_2)) + r_1(U_1(\tilde{N}_1, N_2)) \right. \\
&\quad - r_1(U_1(\tilde{N}_1, \tilde{N}_2)) - \frac{r_{10}N_1}{K_1(T(N_1, N_2))} + \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, N_2))} - \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, N_2))} \\
&\quad \left. + \frac{r_{10}\tilde{N}_1}{K_1(T(\tilde{N}_1, \tilde{N}_2))} - \beta_1(N_2 - \tilde{N}_2) \right] \\
&+ (N_2 - \tilde{N}_2) \left[r_2(U_2(N_1, N_2)) - r_2(U_2(N_1, \tilde{N}_2)) + r_2(U_2(N_1, \tilde{N}_2)) \right. \\
&\quad - r_2(U_2(\tilde{N}_1, \tilde{N}_2)) - \frac{r_{20}N_2}{K_2(T(N_1, N_2))} + \frac{r_{20}\tilde{N}_2}{K_2(T(N_1, \tilde{N}_2))} - \frac{r_{20}\tilde{N}_2}{K_2(T(N_1, \tilde{N}_2))} \\
&\quad \left. + \frac{r_{20}\tilde{N}_2}{K_2(T(\tilde{N}_1, \tilde{N}_2))} - \beta_2(N_1 - \tilde{N}_1) \right] \\
&= (N_1 - \tilde{N}_1)^2 \left[\xi_{11}(N_1, N_2) - \frac{r_{10}}{K_1(T(N_1, N_2))} - r_{10}\tilde{N}_1 \eta_{11}(N_1, N_2) \right] \\
&+ (N_2 - \tilde{N}_2)^2 \left[\xi_{21}(N_1, N_2) - \frac{r_{20}}{K_2(T(N_1, N_2))} - r_{20}\tilde{N}_2 \eta_{21}(N_1, N_2) \right] \\
&+ (N_1 - \tilde{N}_1)(N_2 - \tilde{N}_2) \left[\xi_{12}(\tilde{N}_1, N_2) + \xi_{22}(\tilde{N}_1, N_2) - r_{10}\tilde{N}_1 \eta_{12}(\tilde{N}_1, N_2) \right. \\
&\quad \left. - r_{20}\tilde{N}_2 \eta_{22}(\tilde{N}_1, N_2) - (\beta_1 + \beta_2) \right] \tag{4.4}
\end{aligned}$$

where

$$\xi_{i1}(N_1, N_2) = \begin{cases} [r_i(U_i(N_1, N_2)) - r_i(U_i(\tilde{N}_1, N_2))]/(N_1 - \tilde{N}_1), & N_1 \neq \tilde{N}_1 \\ \left. \frac{\partial r_i}{\partial U_i}(U_i(N_1, N_2)) \frac{\partial U_i}{\partial N_1} \right|_{N_1 = \tilde{N}_1}, & N_1 = \tilde{N}_1 \end{cases},$$

$$\begin{aligned}
\xi_{i2}(\tilde{N}_1, N_2) &= \begin{cases} [r_i(U_i(\tilde{N}_1, N_2)) - r_i(U_i(\tilde{N}_1, \tilde{N}_2))] / (N_2 - \tilde{N}_2), & N_2 \neq \tilde{N}_2 \\ \left. \frac{\partial r_i}{\partial U_i}(U_i(\tilde{N}_1, N_2)) \frac{\partial U_i}{\partial N_2} \right|_{N_2 = \tilde{N}_2}, & N_2 = \tilde{N}_2 \end{cases} \\
\eta_{i1}(N_1, N_2) &= \begin{cases} \frac{\frac{1}{K_i(T(N_1, N_2))} - \frac{1}{K_i(T(\tilde{N}_1, N_2))}}{N_1 - \tilde{N}_1}, & N_1 \neq \tilde{N}_1 \\ - \frac{1}{K_i^2(T(N_1, N_2))} \frac{\partial K_i}{\partial T}(T(N_1, N_2)) \frac{\partial T}{\partial N_1} \Big|_{N_1 = \tilde{N}_1}, & N_1 = \tilde{N}_1 \end{cases} \\
\eta_{i2}(\tilde{N}_1, N_2) &= \begin{cases} \frac{\frac{1}{K_i(T(\tilde{N}_1, N_2))} - \frac{1}{K_i(T(\tilde{N}_1, \tilde{N}_2))}}{N_2 - \tilde{N}_2}, & N_2 \neq \tilde{N}_2 \\ - \frac{1}{K_i^2(T(\tilde{N}_1, N_2))} \frac{\partial K_i}{\partial T}(T(\tilde{N}_1, N_2)) \frac{\partial T}{\partial N_2} \Big|_{N_2 = \tilde{N}_2}, & N_2 = \tilde{N}_2 \end{cases}
\end{aligned} \tag{4.5}$$

Let $r_i(U_i(N_1, N_2))$ and $K_i(T(N_1, N_2))$ satisfy the following conditions

$$\begin{aligned}
K_{mi} \leq K_i(T(N_1, N_2)) \leq K_{i0}, \quad 0 \leq \xi_{i1}(N_1, N_2) \leq \rho_{i1}, \quad 0 \leq \xi_{i2}(\tilde{N}_1, N_2) \leq \rho_{i2}, \\
0 \leq \eta_{i1}(N_1, N_2) \leq k_{i1}, \quad 0 \leq \eta_{i2}(\tilde{N}_1, N_2) \leq k_{i2}, \quad i = 1, 2 \tag{4.6}
\end{aligned}$$

for some positive constants K_{mi} , ρ_{i1} , ρ_{i2} , k_{i1} and k_{i2} .

From (4.5), (4.6) and the mean value theorem, we note that

$$\begin{aligned}
|\xi_{i1}(N_1, N_2)| \leq \rho_{i1}, \quad |\xi_{i2}(\tilde{N}_1, N_2)| \leq \rho_{i2}, \quad |\eta_{i1}(N_1, N_2)| \leq k_{i1}/K_{mi}^2 \quad \text{and} \\
|\eta_{i2}(\tilde{N}_1, N_2)| \leq k_{i2}/K_{mi}^2 \tag{4.7}
\end{aligned}$$

Now $\frac{dV_1}{dt}$ can further be written as

$$\begin{aligned}
\frac{dV_1}{dt} \leq & - (N_1 - \tilde{N}_1)^2 \left[\frac{r_{10}}{K_{m1}} - \rho_{11} \right] - (N_2 - \tilde{N}_2)^2 \left[\frac{r_{20}}{K_{m2}} - \rho_{21} \right] \\
& + (N_1 - \tilde{N}_1) (N_2 - \tilde{N}_2) \left[\rho_{12} + \rho_{22} - (\beta_1 + \beta_2) \right. \\
& \left. - r_{10} \tilde{N}_1 k_{12} / K_{m1}^2 - r_{20} \tilde{N}_2 k_{22} / K_{m2}^2 \right]
\end{aligned} \tag{4.8}$$

Thus $\frac{dV_1}{dt}$ will be negative definite provided

$$\rho_{11} < \frac{r_{10}}{K_{m1}} \tag{4.9a}$$

$$\rho_{21} < \frac{r_{20}}{K_{m2}} \tag{4.9b}$$

$$\begin{aligned}
& \left[\rho_{12} + \rho_{22} - (\beta_1 + \beta_2) - r_{10} \tilde{N}_1 k_{12} / K_{m1}^2 - r_{20} \tilde{N}_2 k_{22} / K_{m2}^2 \right]^2 \\
& < 4 \left(\frac{r_{10}}{K_{m1}} - \rho_{11} \right) \left(\frac{r_{20}}{K_{m2}} - \rho_{21} \right)
\end{aligned} \tag{4.9c}$$

Hence V_1 is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium E_8 and hence this equilibrium is globally asymptotically stable provided the conditions (4.9) are satisfied.

The theorems in § 3 and § 4 show that if the inequalities (3.16) hold, the competing species will settle down to their equilibrium levels the magnitude of which will be lower than their initial carrying capacities and will depend upon its influx and washout rates, the influx rate being dependent upon the emission rate coefficient as well as the equilibrium level of toxicant producing species. The results also suggest that the outcome of the usual competition, in absence of toxicant, may be changed because

in presence of toxicant, some of the conditions (3.7), (3.8), (3.9), (3.16), (4.9) may not be satisfied.

5. NUMERICAL EXAMPLE

We give here a numerical example for the model (2.1). The positive equilibrium point i.e. E_4 has been computed and the stability conditions (both local and global) i.e conditions (3.9) and (3.16) have been checked and it is found that with the following choice of growth rate and carrying capacity functions and with suitable parameter values, all the conditions are satisfied.

Let us take

$$r_1(U_1) = r_{10} - \frac{a_1 U_1}{1 + r_1 U_1} \quad , \quad r_2(U_2) = r_{20} - \frac{a_2 U_2}{1 + r_2 U_2}$$

$$K_1(T) = K_{10} - \frac{b_1 T}{1 + m_1 T} \quad \text{and} \quad K_2(T) = K_{20} - \frac{b_2 T}{1 + m_2 T} \quad (5.1)$$

where

$$r_{10} = 10.0, \quad r_{20} = 11.0, \quad a_1 = 1.0, \quad a_2 = 1.0, \quad b_1 = 1.0, \quad b_2 = 1.0, \quad r_1 = 2.2, \quad r_2 = 3.2, \quad m_1 = 1.02, \quad m_2 = 1.02, \quad K_{10} = 8.09, \quad K_{20} = 7.59$$

Now with this choice of b_i and m_i , we have $\frac{b_i T}{1 + m_i T} < 1$, $i = 1, 2$

Since $K_{mi} \leq K_i(T) \leq K_{i0}$, therefore we can choose K_{mi} as

$$K_{m1} = 6.0, \quad K_{m2} = 5.5. \quad \text{We also note from (5.1) that}$$

$$r'_i(U_i) = - \frac{a_i}{(1 + r_i U_i)^2} \quad \text{and} \quad K'_i(T) = - \frac{b_i}{(1 + m_i T)^2}$$

for $i = 1, 2$

Therefore p_i and q_i can be chosen as 1.0 each ($i = 1, 2$).

$$\text{Choosing } \pi_1 = 0.05, \quad \pi_2 = 0.05, \quad \nu_1 = 0.03, \quad \nu_2 = 0.03, \quad \alpha_1 =$$

0.02, $\alpha_2 = 0.02$, $\beta_1 = 0.5$, $\beta_2 = 0.3$, $\delta_0 = 16.0$, $\delta_1 = 17.0$, $\delta_2 = 16.5$, $\lambda = 0.2$, the equilibrium values N_1^* , N_2^* , T^* , U_1^* and U_2^* are computed as

$$N_1^* = 7.590891, N_2^* = 7.500000, T^* = 0.093131, U_1^* = 0.000821, U_2^* = 0.000835.$$

6. CONCLUSIONS

In this Chapter, a mathematical model is proposed and analyzed to study the effect of a toxicant in a competitive system when the toxicant is being produced by one of the species itself. It is assumed that the uptake concentration of toxicant by each competing species is different and their growth rates decrease as the uptake concentration of the toxicant increases. However, the maximum population density of the competing biological species which the environment can support decreases as the environmental concentration of the toxicant increases. It is also considered that the growth rate and maximum population density of each species decrease as the density of the other species increases. It is shown that the competitive species will settle down to its steady state level under certain conditions such that the magnitude of the competitive species will be lower than their initial carrying capacities and the magnitude of the toxicant will depend upon its influx and washout rates. It is also pointed out that the survival of both the competing species will be threatened if the toxicant continues to be produced unabatedly by the species. The analysis in this Chapter also suggests that the outcome of the usual competition may change in presence of a toxicant.

CHAPTER IX

EFFECT OF A TOXICANT ON A BIOLOGICAL POPULATION CAUSING SEVERE SYMPTOMS ON A SUBCLASS

1. INTRODUCTION

In previous chapters, we have studied the effect of one or more toxicant~~s~~ on a biological population affecting all the individuals of the population uniformly. However, it may happen that the effect of toxicant on some members of the population is more severe than the others and hence the subclass of such members of the population affected severely may exhibit abnormal symptoms such as deformity in shape, size, etc. This is possible even if all the individuals of the population are exposed to the toxicant for the same duration as in the case of aquatic systems (Hamilton and Saether, 1971; Woin and Bronmark, 1992; Cushman, 1984; Warwick, 1985; Hartwell et al, 1993; Dickman and Rygiel, 1996) and in terrestrial ecosystems, affecting leaf size and causing necrotic markings (lesion), etc. in plants (Kozlowski, 1975, 1980). For example, Hartwell et al (1993) studied the growth of *Eurytemora affinis* (Copepoda) in flow through chambers at different locations of polluted sites in Chesapeake Bay tributaries and found that growth rate and fecundity may be chosen as indicators of water quality at appropriate locations and in between the locations. Woin and Bronmark (1992) studied the effect of DDT and MCPA on reproduction of snail collected from eutrophic pond in southern Sweden and showed that these pollutants may have no effect on

mortality but have profound effect on the distribution and abundance of the species through a reduction in the reproductive potential. Dickman and Rygiel (1996) studied the effects of heavy metals and oily wastes discharged from a stainless steel company in the Niagara River on an invertebrate population of midge (chironomid) larvae and found that 26 % of the chironomids from sites located 10 to 800 m down stream were deformed.

It may be noted here that till now, the phenomenon where a subclass of the population gets affected severely and shows symptoms such as deformity, etc. has not been studied using mathematical models. In this chapter, therefore, we propose and analyze a mathematical model to study the effect of a toxicant on a biological population such that a subclass of the total population shows abnormal symptoms. It has been assumed here that the toxicant is being emitted in to the environment by some external sources.

2. MATHEMATICAL MODEL

We consider a logistically growing biological species which is being affected by a toxicant in the environment. This toxicant affects a subclass of the total population acutely showing severe symptoms such as changes in shape, size, causing deformity, necrotic markings, reduction in reproduction capability, etc. We assume that this subclass is not capable of reproduction and the growth rate of its density is proportional to the reduction of growth rate of the species. Using the similar arguments as Freedman and Shukla (1991), the system is assumed to be governed by following non linear differential equations :

$$\begin{aligned}
\frac{dN}{dt} &= r(U) N - \frac{r_0 N^2}{K(T)} \\
\frac{dN_d}{dt} &= k \left[r_0 - r(U) \right] N - r_2 N_d \\
\frac{dT}{dt} &= Q(t) - \delta T - \alpha TN + \pi \nu NU \\
\frac{dU}{dt} &= -\beta U + \alpha TN - \nu NU
\end{aligned}
\tag{2.1}$$

$$N(0) \geq 0, N_d(0) \geq 0, T(0) \geq 0, U(0) \geq cN(0), 0 \leq \pi \leq 1, c > 0$$

In model (2.1), $N(t)$ is the density of the species which is affected by a toxicant with environmental concentration $T(t)$. $N_d(t)$ is assumed to be the density of the subclass of the population which is affected severely by this toxicant. The toxicant is assumed to be emitted in to the environment by some external sources with a cumulative rate $Q(t)$. $U(t)$ is the uptake concentration of the toxicant by the species with density $N(t)$. δ is the depletion rate coefficient of toxicant from the environment due to some natural factors. β is the natural depletion rate coefficient of $U(t)$. The growth rate of uptake concentration $U(t)$ in the biological species increases by an amount αTN which is the same as the rate of depletion of environmental concentration $T(t)$, where $\alpha > 0$ is the uptake rate coefficient. $\nu > 0$ is the depletion rate coefficient of $U(t)$ due to decay of some members of N i.e. νNU and a fraction π of which may reenter into the environment. All the constants appearing here are positive.

In the model, the growth rate function $r(U)$ is assumed to satisfy the following properties,

$$r(0) = r_0 > 0, r'(U) < 0 \text{ for all } U \geq 0 \tag{2.2a}$$

In the model (2.1), we note that the abnormal behavior exhibited by a subclass of the population is due to the uptake of the toxicant by the species and hence the growth rate of $N_d(t)$ is taken as proportional to " $r_0 - r(U)$ " which is the decrease in the growth rate of the species of density $N(t)$. k is a positive constant which denotes the fraction of the subclass which survives and r_2 is the mortality rate of the severely affected population.

The function $K(T)$ denotes the maximum biomass density of the biological population which the environment can support in the presence of the toxicant and we assume that it satisfies the following property,

$$K(0) = K_0 > 0, K'(T) < 0 \text{ for all } T > 0 \quad (2.2b)$$

Now, we analyze model (2.1) in the following two cases:

$Q(t) = 0$ (instantaneous emission) and $Q(t) = Q_0 > 0$ (a constant)

3. MATHEMATICAL ANALYSIS

3.1 THE CASE WHEN $Q(t) = 0$ (INSTANTANEOUS EMISSION)

In this case, the toxicant is discharged in to the environment at $t = 0$ with concentration $T = T_0$. The model (2.1) has two equilibrium points, namely $E_1 = (0, 0, 0, 0)$ and $E_2 = (K_0, 0, 0, 0)$. The existence of E_1 and E_2 are obvious.

The local stability behavior of the equilibria E_1 and E_2 can be seen by computing variational matrices. The corresponding matrices are given by

$$M_1 = M|_{E_1} = \begin{bmatrix} r_0 & 0 & 0 & 0 \\ 0 & -r_2 & 0 & 0 \\ 0 & 0 & -\delta & 0 \\ 0 & 0 & 0 & -\beta \end{bmatrix},$$

$$M_2 = M|_{E_2} = \begin{bmatrix} -r_0 & 0 & r_0 K'(0) & r'(0) K_0 \\ r_1 & -r_2 & 0 & -k K_0 r'(0) \\ 0 & 0 & -(\delta + \alpha K_0) & \pi \nu K_0 \\ 0 & 0 & \alpha K_0 & -(\beta + \nu K_0) \end{bmatrix}$$

From M_1 it follows that E_1 is a saddle point whose stable manifold is locally in the N_d -T-U plane and unstable in the N direction.

From M_2 , it can be checked that its two eigen values in N and N_d directions are $-r_0$ and $-r_2$. The other two eigen values (in T and U directions) will have negative real parts provided

$$\begin{vmatrix} -(\delta + \alpha K_0) & \pi \nu K_0 \\ \alpha K_0 & -(\beta + \nu K_0) \end{vmatrix} > 0$$

$$\text{i.e. } \beta \delta + (\alpha \beta + \nu \delta) K_0 + (1 - \pi) \alpha \nu K_0^2 > 0$$

which is satisfied. Hence E_2 is locally asymptotically stable without any condition.

In the following theorem we give the global asymptotic stability behavior of E_2 .

THEOREM 3.1 If $N(0) > 0$, then E_2 is globally asymptotically stable.

PROOF Using a comparison theorem, from the first equation of (2.1), we have

$$\frac{dN}{dt} \leq r_0 N - r_0 \frac{N^2}{K_0} = r_0 \left(1 - \frac{N}{K_0}\right) N$$

Thus, $\limsup_{t \rightarrow \infty} N(t) \leq K_0$,

Adding last two equations of (2.1) we get

$$\frac{dT}{dt} + \frac{dU}{dt} = -\delta T - \beta U - (1 - \pi)\nu NU$$

$$\leq -\delta_m (T + U), \text{ where } \delta_m = \min \{\delta, \beta\}$$

which gives $\limsup_{t \rightarrow \infty} T(t) = 0 = \limsup_{t \rightarrow \infty} U(t)$,

Then from the second equation of (2.1), we have

$$\frac{dN_d}{dt} \leq k \left[r_0 - r(U_{\min}) \right] K_0 - r_2 N_d,$$

where U_{\min} is the minimum value of U attained. But from the above, it is clear that $U_{\min} = 0$ and hence $r(U_{\min}) = r_0$, which in turn gives

$$\frac{dN_d}{dt} \leq -r_2 N_d$$

$$\Rightarrow \limsup_{t \rightarrow \infty} N_d(t) = 0.$$

Thus, the system is dissipative and hence the theorem.

The above theorem implies that under instantaneous emission of a toxicant, the toxicant may be washed out completely from the environment and the species settles down to original carrying capacity but it may take some time to attain this state.

3.2 THE CASE WHEN $Q(t) = Q_0$ (A CONSTANT)

In this case again, the model (2.1) has two equilibrium points, namely $E_3 = (0, 0, \frac{Q_0}{\delta_0}, 0)$ and $E_4 = (N^*, N_d^*, T^*, U^*)$. The existence of E_3 is obvious. The existence of E_4 is shown as follows:

Here N^* , N_d^* , T^* and U^* are the positive solutions of the following algebraic equations:

$$N = \frac{r(U)K(T)}{r_0} \quad (3.1a)$$

$$N_d = \frac{k(r_0 - r(U))}{r_2} N \quad (3.1b)$$

$$T = \frac{Q_0 (\beta + \nu N)}{f(N)} = h(N) \quad (\text{say}) \quad (3.1c)$$

$$U = \frac{Q_0 \alpha N}{f(N)} = g(N) \quad (\text{say}) \quad (3.1d)$$

$$\text{where } f(N) = \beta\delta + (\alpha\beta + \nu\delta)N + (1 - \pi) \alpha\nu N^2 > 0 \quad (3.1e)$$

From (3.1), we note that T and U increase as Q_0 increases. Since $r(U)$ is a decreasing function of U , therefore, $r(U)$ decreases as Q_0 increases and hence N_d increases as Q_0 increases.

Now taking

$$F(N) = r_0 N - r(g(N)) K(h(N)) \quad (3.2a)$$

We note that $F(0) < 0$ and $F(K_0) > 0$. This shows that the function $F(N)$ has a root say N^* in the interval $0 < N^* < K_0$. Now for the uniqueness of N^* , we must have $F'(N) > 0$ in the interval $0 < N < K_0$, i.e.

$$r_0 - \left[r(g(N)) \frac{dK}{dT} \frac{dh}{dN} + K(h(N)) \frac{dr}{dU} \frac{dg}{dN} \right] > 0 \quad (3.2b)$$

Knowing the value of N^* , the values of N_d^* , T^* and U^* can be computed using equations (3.1b), (3.1c) and (3.1d) respectively.

The local stability behavior of the equilibria E_3 and E_4 can be seen by computing variational matrices corresponding to them. These matrices are given by

$$M_3 = M|_{E_3} = \begin{bmatrix} r_0 & 0 & 0 & 0 \\ 0 & -r_2 & 0 & 0 \\ -\frac{\alpha Q_0}{\delta} & 0 & -\delta & 0 \\ \frac{\alpha Q_0}{\delta} & 0 & 0 & -\beta \end{bmatrix},$$

$$M_4 = M|_{E_4} = \begin{bmatrix} -\frac{r_0 N^*}{K(T^*)} & 0 & \frac{r_0 N^{*2}}{K^2(T^*)} K'(T^*) & N^* r'(U^*) \\ k(r_0 - r(U)) & -r_2 & 0 & -kN^* r'(U^*) \\ -(\alpha T^* - \pi \nu U^*) & 0 & -(\delta + \alpha N^*) & \pi \nu N^* \\ (\alpha T^* - \nu U^*) & 0 & \alpha N^* & -(\beta + \nu N^*) \end{bmatrix}$$

From M_3 , it follows that E_3 is a saddle point whose stable manifold is locally in the N_d - T - U plane and it is unstable in the N - direction. The stability behavior of E_4 is established using the Routh - Hurwitz criterion. The local asymptotic behavior of E_4 is characterized in the following theorem.

THEOREM 3.2 Let the following inequality hold

$$(\delta + \alpha N^*) > \frac{N^*}{K(T^*)} (\alpha T^* - \pi \nu U^*) (-K'(T^*)) \quad (3.3)$$

then E_4 is locally asymptotically stable.

The proof of this theorem follows from Routh Hurwitz criterion using M_4 .

Before establishing the global asymptotic stability of E_4 , we first need the following lemma which establishes the region of attraction for E_4 .

LEMMA 3.1 The region

$$\Omega_1 = \left\{ (N, N_d, T, U) : 0 \leq N \leq K_0, 0 \leq N_d \leq \frac{kr_0 K_0}{r_2}, \right. \\ \left. 0 \leq T(t) + U(t) \leq \frac{Q_0}{\delta_m} \right\}$$

where $\delta_m = \min(\delta, \beta)$

attracts all solutions initiating in the interior of the positive orthant.

PROOF: From the first equation of (2.1) we have

$$\frac{dN}{dt} \leq r_0 N - r_0 \frac{N^2}{K_0} = r_0 \left(1 - \frac{N}{K_0}\right) N$$

Thus $\limsup_{t \rightarrow \infty} N(t) \leq K_0$.

From the second equation of (2.1), we get,

$$\frac{dN_d}{dt} \leq kr_0 N - r_2 N_d \leq kr_0 K_0 - r_2 N_d$$

$$\Rightarrow \limsup_{t \rightarrow \infty} N_d(t) \leq \frac{kr_0 K_0}{r_2}.$$

Adding the last two equations of (2.1), we get

$$\frac{dT}{dt} + \frac{dU}{dt} = Q_0 - \delta T - \beta U - (1 - \pi)\nu NU$$

$$\leq Q_0 - \delta_m (T + U), \text{ where } \delta_m = \min \{ \delta, \beta \}$$

which gives $\limsup_{t \rightarrow \infty} [T(t) + U(t)] = \frac{Q_0}{\delta_m}$, proving the lemma.

The following theorem characterizes the global stability behavior of the equilibrium point E_4 .

THEOREM 3.3 In addition to the assumptions (2.2a-c), let the functions $r(U)$ and $K(T)$ satisfy the following conditions in Ω_1

$$\left| r'(U) \right| \leq \rho, \quad K_m \leq K(T) \leq K_0, \quad \left| K'(T) \right| \leq k \quad (3.4)$$

where ρ , K_m and k are positive constants. Then if the following inequalities hold in Ω_1

$$k^2 \left[r_0 - r(U^*) \right]^2 < \frac{2}{3} \frac{r_0}{K(T^*)} r_2 \quad (3.5a)$$

$$\left[\frac{r_0 K_0}{K_m^2} k + (\alpha + \pi\nu) \frac{Q_0}{\delta_m} \right]^2 < \frac{2}{3} \frac{r_0}{K(T^*)} (\delta + \alpha N^*) \quad (3.5b)$$

$$\left[\rho + (\alpha + \nu) \frac{Q_0}{\delta_m} \right]^2 < \frac{4}{9} \frac{r_0}{K(T^*)} (\beta + \nu N^*) \quad (3.5c)$$

$$\left[k K_0 \rho \right]^2 < \frac{2}{3} r_2 (\beta + \nu N^*) \quad (3.5d)$$

$$\left[(\pi\nu + \alpha) N^* \right]^2 < \frac{2}{3} (\delta + \alpha N^*) (\beta + \nu N^*) \quad (3.5e)$$

Then E_4 is globally asymptotically stable with respect to all solutions initiating in the interior of the positive orthant.

PROOF : Consider the following positive definite function around E_4 ,

$$W(N, N_d, T, U) = \left\{ N - N^* - N^* \ln \left(\frac{N}{N^*} \right) \right\} + \frac{1}{2} (N_d - N_d^*)^2 + \frac{1}{2} (T - T^*)^2 + \frac{1}{2} (U - U^*)^2 \quad (3.6a)$$

The derivative of W with respect to t , along the solutions of the system (2.1) is given by

$$\frac{dW}{dt} = (N - N^*) \frac{\dot{N}}{N} + (N_d - N_d^*) \dot{N}_d + (T - T^*) \dot{T} + (U - U^*) \dot{U}$$

Substituting the values of \dot{N} , \dot{N}_d , \dot{T} and \dot{U} from equations (2.1) in the above, we get

$$\begin{aligned} \frac{dW}{dt} = & (N - N^*) \left[r(U) - \frac{r_0 N}{K(T)} \right] + (N_d - N_d^*) \left[k(r_0 - r(U))N - r_2 N_d \right] \\ & + (T - T^*) \left[Q_0 - \delta T - \alpha TN + \pi \nu NU \right] \\ & + (U - U^*) \left[-\beta U + \alpha TN - \nu NU \right] \end{aligned} \quad (3.6b)$$

Using (3.1) and simplifying, we get after a little algebraic manipulation

$$\begin{aligned} \frac{dW}{dt} = & - \frac{r_0}{K(T^*)} (N - N^*)^2 - r_2 (N_d - N_d^*)^2 - (\delta + \alpha N^*) (T - T^*)^2 \\ & - (\beta + \nu N^*) (U - U^*)^2 + (N - N^*) (N_d - N_d^*) \left\{ k(r_0 - r(U^*)) \right\} \\ & + (N - N^*) (T - T^*) \left\{ -r_0 N \eta(T) + \alpha T - \pi \nu U \right\} \\ & + (N - N^*) (U - U^*) \left\{ \xi(U) + \alpha T - \nu U \right\} \\ & + (N_d - N_d^*) (U - U^*) \left\{ -k N \xi(U) \right\} \\ & + (T - T^*) (U - U^*) \left\{ (\pi \nu + \alpha) N^* \right\} \end{aligned}$$

where

$$\xi(U) = \begin{cases} \frac{r(U) - r(U^*)}{(U - U^*)} & , U \neq U^* \\ r'(U^*) & , U = U^* \end{cases} \quad (3.6c)$$

and

$$\eta(T) = \begin{cases} \frac{\frac{1}{K(T)} - \frac{1}{K(T^*)}}{(T - T^*)} & , T \neq T^* \\ -\frac{K'(T^*)}{K^2(T^*)} & , T = T^* \end{cases} \quad (3.6d)$$

Thus, $\frac{dW}{dt}$ can further be written as sum of the quadratics

$$\begin{aligned} \frac{dW}{dt} = & -\frac{1}{2} b_{11} (N - N^*)^2 + b_{12} (N - N^*) (N_d - N_d^*) - \frac{1}{2} b_{22} (N_d - N_d^*)^2 \\ & - \frac{1}{2} b_{11} (N - N^*)^2 + b_{13} (N - N^*) (T - T^*) - \frac{1}{2} b_{33} (T - T^*)^2 \\ & - \frac{1}{2} b_{11} (N - N^*)^2 + b_{14} (N - N^*) (U - U^*) - \frac{1}{2} b_{44} (U - U^*)^2 \\ & - \frac{1}{2} b_{22} (N_d - N_d^*)^2 + b_{24} (N_d - N_d^*) (U - U^*) - \frac{1}{2} b_{44} (U - U^*)^2 \\ & - \frac{1}{2} b_{33} (T - T^*)^2 + b_{34} (T - T^*) (U - U^*) - \frac{1}{2} b_{44} (U - U^*)^2 \end{aligned} \quad (3.6e)$$

where

$$\begin{aligned} b_{11} &= \frac{2}{3} \frac{r_0}{K(T^*)} , \quad b_{22} = r_2 , \quad b_{33} = (\delta + \alpha N^*) , \quad b_{44} = \frac{2}{3} (\beta + \nu N^*) , \\ b_{12} &= k \left[r_0 - r(U^*) \right] , \quad b_{13} = - \left(r_0 N \eta(T) + \alpha T - \pi \nu U \right) , \\ b_{14} &= \xi(U) + \alpha T - \nu U , \quad b_{24} = -kN \xi(U) , \quad b_{34} = (\pi \nu + \alpha) \cdot N^* \end{aligned} \quad (3.6f)$$

Thus $\frac{dW}{dt}$ will be negative definite provided

$$b_{12}^2 < b_{11}b_{22} , \quad b_{13}^2 < b_{11}b_{33} , \quad b_{14}^2 < b_{11}b_{44},$$

$$b_{24}^2 < b_{22}b_{44} \text{ and } b_{34}^2 < b_{33}b_{44}$$

which give the same inequalities as in equations (3.5a) - (3.5e).

Hence W is a Liapunov's function with respect to E_4 whose domain contains Ω_1 and therefore E_4 is globally asymptotically stable. Hence the theorem.

4. A QUASI STEADY STATE ANALYSIS OF CONCENTRATIONS OF TOXICANT (FOR THE CASE OF CONSTANT EMISSION, i.e. $Q(t) = Q_0$)

In this case, we assume that the dynamics of the environmental and uptake concentrations of the toxicant are so fast such that their equilibria are attained with the densities of both the normal and abnormal species almost instantaneously. In such a case, we assume :

$$\frac{dN_d}{dt} \approx 0, \quad \frac{dT}{dt} \approx 0 \quad \text{and} \quad \frac{dU}{dt} \approx 0 \quad \text{for all } t \geq 0.$$

From last three equations of (2.1), we then have

$$N_d \approx \frac{k(r_0 - r(g(N)))}{r_2} N \quad (4.1a)$$

$$T \approx \frac{Q_0 (\beta + \nu N)}{f(N)} = h(N) \quad (\text{say}) \quad (4.1b)$$

$$U \approx \frac{Q_0 \alpha N}{f(N)} = g(N) \quad (\text{say}) \quad (4.1c)$$

where $f(N)$ is the same as defined in equation (3.1e).

We note that T , U and N_d are expressed as functions of N and they increase as Q_0 increases and hence $r(U(N))$ and $K(T(N))$ decrease with Q_0 .

In this case the model (2.1) reduces to

$$\frac{dN}{dt} = \left[r(U(N)) - \frac{r_0 N}{K(T(N))} \right] N \quad (4.2)$$

with $N(0) = N_0 \geq 0$.

The above equation (4.2), is a generalized logistic equation.

Thus, the above system has only two equilibrium points $N = 0$ and $N = N^\circ$ where N° is obtained by solving (3.2a) i.e.

$$F(N) = 0$$

which exists uniquely under the same condition as shown in the previous section.

Using comparison theorem, it can be noted that from (4.2) that

$$\frac{dN}{dt} \leq r_0 \left(1 - \frac{N}{K_0} \right) N \quad (4.3)$$

This implies that $0 < N^\circ < K_0$.

Since U and T increase as Q_0 increases, therefore, N° decreases as Q_0 increases. Further if Q_0 becomes very large then N° may even tend to zero. This implies that the species may not survive for large emission rates and only abnormal subclass survives.

We can check that $N = 0$ is unstable. To find the behavior of N° , we proceed as follows:

Consider the following positive definite function about N°

$$V(N) = (N - N^\circ - N^\circ \ln \frac{N}{N^\circ})$$

Differentiating V with respect to t along the solution of the model (4.2), we get

$$\frac{dV}{dt} = (N - N^\circ) \left[r(U(N)) - \frac{r_0 N}{K(T(N))} \right]$$

$$\begin{aligned}
&= (N - N^\circ) \left[r(U(N)) - r(U(N^\circ)) - \frac{r_0^N}{K(T(N))} + \frac{r_0^{N^\circ}}{K(T(N^\circ))} \right. \\
&\quad \left. - \frac{r_0^N}{K(T(N^\circ))} + \frac{r_0^{N^\circ}}{K(T(N^\circ))} \right] \\
&= (N - N^\circ)^2 \left[\xi_1(N) - r_0^N \eta_1(N) - \frac{r_0}{K(T(N^\circ))} \right] \tag{4.4}
\end{aligned}$$

where

$$\begin{aligned}
\xi_1(N) &= \begin{cases} [r(U(N)) - r(U(N^\circ))]/(N - N^\circ) & , \quad N \neq N^\circ \\ \left. \frac{\partial r}{\partial U} \frac{dU}{dN} \right|_{N = N^\circ} & , \quad N = N^\circ \end{cases} \\
\eta_1(N) &= \begin{cases} \frac{\frac{1}{K(T(N))} - \frac{1}{K(T(N^\circ))}}{N - N^\circ} & , \quad N \neq N^\circ \\ - \frac{1}{K^2(T(N))} \left. \frac{\partial K}{\partial T} \frac{dT}{dN} \right|_{N = N^\circ} & , \quad N = N^\circ \end{cases} \tag{4.5}
\end{aligned}$$

Let $r(U(N))$ and $K(T(N))$ satisfy the following conditions

$$K_{m1} \leq K(T(N)) \leq K_0, \quad 0 \leq - \frac{\partial r}{\partial U} \frac{dU}{dN}(N^\circ) \leq \rho_1, \quad 0 \leq - \frac{\partial K}{\partial T} \frac{dT}{dN}(N^\circ) \leq k_1 \tag{4.6}$$

for some positive constants K_{m1} , ρ_1 and k_1 .

From (4.5), (4.6) and the mean value theorem, we note that

$$|\xi_1(N)| \leq \rho_1 \quad \text{and} \quad |\eta_1(N)| \leq k_1/K_{m1}^2 \tag{4.7}$$

Now $\frac{dV}{dt}$ can further be written as

$$\frac{dV}{dt} \leq (N - N^\circ)^2 \left[\rho_1 - \frac{r_0 K_0 k_1}{K_{m1}^2} - \frac{r_0}{K(T(N^\circ))} \right]$$

Thus $\frac{dV}{dt}$ will be negative definite provided

$$\rho_1 < \frac{r_0 K_0 k_1}{K_{m1}^2} + \frac{r_0}{K(T(N^\circ))} \quad (4.8)$$

Hence V is a Lyapunov's function (La Salle and Lefschetz, 1961) with respect to the equilibrium $N = N^\circ$ and hence this equilibrium is globally asymptotically stable provided the condition (4.8) is satisfied.

The theorems in § 3 and § 4 imply that under the constant emission of toxicant in the environment, under certain conditions, the species would settle down to its equilibrium value which is less than its original carrying capacity. A subclass of this species, severely affected and showing abnormal symptoms, would also attain its equilibrium value the magnitude of which increases as the rate of constant emission of the toxicant increases. If the rate of emission is very large, even all the species may become abnormal.

5. NUMERICAL EXAMPLE

We give here a numerical example for the model (2.1), in the case of constant emission. The positive equilibrium point i.e. E_4 has been computed and the stability conditions (both local and global) i.e conditions (3.3) and (3.5) have been checked and it is found that with the following choice of growth rate and carrying

capacity functions and with suitable parameter values, all the conditions are satisfied.

Let us take

$$r(U) = r_0 - \frac{a_1 U}{1 + r_1 U} \quad \text{and} \quad K(T) = K_0 - \frac{b_1 T}{1 + m_1 T} \quad (5.1)$$

where

$$r_0 = 12.0, \quad a_1 = 1.0, \quad b_1 = 1.0, \quad r_1 = 0.2, \quad m_1 = 1.02, \quad K_0 = 6.859.$$

Now with this choice of b_1 and m_1 , we have $\frac{b_1 T}{1 + m_1 T} < 1$.

Since $K_m \leq K(T) \leq K_0$, therefore we can choose K_m as $K_m = 4.5$.

We also note from (5.1) that

$$r'(U) = - \frac{a_1}{(1 + r_1 U)^2} \quad \text{and} \quad K'(T) = - \frac{b_1}{(1 + m_1 T)^2}$$

Therefore ρ and k can be chosen as 1.0 each.

Choosing $r_2 = 10.0$, $k = 0.5$, $\pi = 0.05$, $\nu = 0.03$, $\alpha = 0.2$, $\beta = 12.0$, $\delta = 14.0$, $Q_0 = 5.0$, the equilibrium values N^* , N_d^* , T^* and U^* are computed as

$$N^* = 6.594796, \quad N_d^* = 0.011557, \quad T^* = 0.326416, \quad U^* = 0.035296.$$

For the choices, mentioned above, the stability conditions (3.3) and (3.5) are satisfied.

6. CONCLUSIONS

In this Chapter, a mathematical model is proposed and analyzed to study the effect of a toxicant on a biological species, a subclass of which is severely affected showing abnormal symptoms such as deformity, necrosis, etc.

It has been shown that under instantaneous emission of the toxicant, the system gets restored to its original state but after a long time. However, for constant emission, under certain conditions, the species would settle down to its equilibrium value whose magnitude is less than its original carrying capacity. It is also found that a subclass of this species, which is severely affected and shows abnormal symptoms, also settles down to its equilibrium level but the magnitude of this equilibrium level increases as the emission rate of the toxicant increases. For large emission rate it may happen that the entire population gets severely affected and become abnormal (different from the original species).

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